UNIVERSITÉ DU QUÉBEC À RIMOUSKI

DISPARITÉ MORPHOLOGIQUE ET MODULARITÉ DES NAGEOIRES MÉDIANES ET PAIRES CHEZ LES VERTÉBRÉS BASAUX

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OLIVIER LAROUCHE

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AVANT-PROPOS

« *There once were two watchmakers, named Hora and Tempus, who manufactured very fine watches. Both of them were highly regarded, and the phones in their workshops rang frequently - new customers were constantly calling them (…) The watches the men made consisted of about 1000 parts each. Tempus had so constructed his that if he had one partly assembled and had to put it down - to answer the phone say - it immediately fell to pieces and had to be reassembled from the elements (…) The watches that Hora made were no less complex than those of Tempus. But he had designed them so that he could put together subassemblies of about ten elements each. Ten of these subassemblies, again, could be put together into a larger subassembly ; and a system of ten of the latter subassemblies constituted the whole watch. Hence, when Hora had to put down a partly assembled watch in order to answer the phone, he lost only a small part of his work (…)* »

(Simon 1962, p. 468)

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RÉSUMÉ

Les organismes vivants sont morphologiquement très diversifiés. Chez les poissons, cette disparité morphologique relève entre autres de différences dans la configuration des nageoires, notamment quant au nombre de nageoires présentes et à leurs positions relatives sur le corps. L'une des propriétés organisationnelles du vivant qui pourrait favoriser l'accumulation de disparité morphologique est la modularité. La modularité stipule que les organismes sont constitués de sous-unités hautement cohésives appelées "modules". Puisque les modules sont quasi-indépendants les uns par rapport aux autres au cours du développement ou de l'évolution, ils peuvent individuellement être optimisés sans affecter l'intégrité du reste de l'organisme. L'objectif général de cette thèse doctorale était donc d'étudier les patrons de covariation quant à la présence/absence des nageoires et à la position relative que chacune d'elles occupe sur le corps des poissons afin d'identifier des modules aux échelles micro- et macroévolutives.

Le premier objectif était d'analyser la disparité morphologique et la covariance dans la présence/absence des nageoires à une échelle macroévolutive. Un super-arbre phylogénétique incluant 144 ordres de poissons actuels et fossiles a été produit, puis les caractères de présence/absence des nageoires ont été superposés sur ce super-arbre. La répartition phylogénétique des caractères suggère que les nageoires médianes et paires seraient apparues d'abord sous la forme de structures allongées qui auraient éventuellement été modifiées en nageoires aux insertions plus exiguës. Une combinaison d'analyses exploratoires et de tests d'hypothèses ont aussi permis de démontrer que certaines nageoires (dorsale/anale, pectorales/pelviennes) covarient davantage en termes de présence/absence, ce qui suggère qu'elles forment des modules évolutifs.

Le deuxième objectif était d'analyser les patrons de covariation en termes de positions relatives des nageoires sur le corps du poisson à l'échelle microévolutive. Pour ce volet, deux espèces de Cyprinidae (*Danio rerio* et *Chrosomus eos*) ont été utilisés comme organismes modèles. À l'aide d'une approche en morphométrie géométrique, quatre méthodes ont été utilisées afin de tester et d'évaluer la qualité d'ajustement d'une série d'hypothèses de modularité aux données observées. Les hypothèses de modularité les mieux supportées suggèrent que la région postérieure du tronc et de la queue, incluant les nageoires dorsale, anale et caudale, forme un module variationnel. Ce résultat s'explique en partie par des contraintes fonctionnelles engendrées par un mode de locomotion de type subcaranguiforme. Un module variationnel des nageoires paires est également supporté, mais moins fortement que celui du tronc postérieur et de la queue. Les modules variationnels identifiés ne correspondent pas exactement aux modules suggérés par les données développementales. Cette non-concordance pourrait résulter de contraintes fonctionnelles et/ou des effets de différents processus développementaux

qui se superposent au cours de l'ontogénie, embrouillant ainsi le signal de chacun des processus développementaux considérés individuellement.

Le troisième objectif était d'analyser les patrons de covariation en termes de positions relatives des nageoires sur le corps du poisson à l'échelle macroévolutive. Ici aussi, une approche en morphométrie géométrique a été préconisée en utilisant cette fois un échantillon de 58 espèces d'actinoptérygiens couvrant un large spectre phylogénétique. Parmi les hypothèses de modularité les mieux supportées, l'une d'elles subdivise le corps du poisson en trois modules évolutifs : la tête, le tronc et la queue. Or, le module du tronc, qui inclut les points d'insertion de toutes les nageoires sauf la caudale, est caractérisé par un taux d'évolution significativement supérieur aux deux autres modules, en plus de présenter une disparité morphologique plus importante. Ceci suggère qu'une relation existe entre la modularité et la disparité morphologique, par l'entremise de changements dans les taux d'évolution morphologique. Les résultats suggèrent aussi qu'il existe à la fois des similitudes et des différences quant aux patrons d'intégration morphologique et de modularité observés entre les échelles micro- et macroévolutives. Les patrons identifiés à l'échelle des actinoptérygiens pourraient refléter un amalgame des patrons inhérents à un certain nombre de lignées évolutives appartenant à ce clade.

Une conclusion importante concernant l'ensemble des résultats de cette étude est qu'il existe une correspondance partielle entre les patrons d'intégration morphologique et de modularité identifiés aux échelles micro- et macroévolutive. Puisque les hypothèses de modularité qui ont été testées sont largement basées sur des observations développementales, ceci implique une relation entre des modules développementaux, variationnels et évolutifs. Ce faisant, cela unit des processus qui se déroulent à l'échelle des individus, des populations et des espèces.

MOTS-CLÉS : disparité morphologique, modularité, poissons, nageoires médianes et paires, morphométrie géométrique.

ABSTRACT

Biological organisms are morphologically highly disparate. In fishes, this morphological disparity relates in part to differences in fin configurations, notably in terms of the number of fins present and their relative positions along the body axis. A property of biological systems that is thought to favor the emergence of morphological disparity is modularity. Modularity postulates that organisms can be decomposed into a number of highly cohesive sub-units termed "modules." Because modules behave as quasi-independent units during development and/or evolution, they can be individually optimized while minimally impacting other aspects of the organism. The principal objective of this doctoral thesis was to investigate patterns of covariation in the presence/absence of fins and in their relative positioning on the body in order to identify fin modules at both micro- and macroevolutionary scales.

The first objective was to analyse the disparity in fin configurations as well as patterns of covariation in the presence/absence of fins at a macroevolutionary scale. A phylogenetic supertree including 144 extant and extinct orders of fishes was produced, and the fin presence/absence data was mapped onto the supertree. The phylogenetic distribution of fin characters suggests that both median and paired fins would have appeared first as elongated structures before they were modified into fins with narrower bases. The results from a combination of exploratory analyses and hypothesis tests showed that some sets of fins (dorsal/anal fins, pectoral/pelvic fins) covary more strongly in their presence/absence, which suggests that they form evolutionary modules.

The second objective was to analyse patterns of covariation in the relative positioning of fins on the fish's body at a microevolutionary scale. For this second chapter of the thesis, two species of the Cyprinidae (*Danio rerio* and *Chrosomus eos*) were used as model organisms. Using a geometric morphometry approach, four methods were used to assess the fit of a series of hypotheses of modularity to the observed data. The best-supported hypotheses of modularity suggest that the posterior trunk and tail, including the bases of the dorsal, anal and caudal fins, form a variational module. This result can be explained in part by functional constraints resulting from the use of a subcaranguiform swimming mode in these two species. A paired fins variational module is also supported, although less so than the posterior trunk and tail module. These variational modules that have been identified do not show a perfect correspondence to the modules that were expected based on developmental data. Discrepancies between developmental and variational modules could stem from functional constraints and/or from the effects of multiple developmental processes that overlap temporally and spatially during ontogeny, the result being that the signal from individual developmental processes can be partly overwritten.

The third objective was to analyse patterns of covariation in the relative positioning of fins on the fish's body at a macroevolutionary scale. Here as well, methods of geometric morphometry were applied using a phylogenetically broad sample of 58 actinopterygian species. One of the best-supported hypotheses of modularity across methods subdivides the fish's body into three evolutionary modules: the head, the trunk, and the tail. Furthermore, the trunk module, which comprises the insertion points of all of the fins excepting the caudal fin, has a significantly higher rate of morphological evolution than the head and tail modules and is also much more disparate. This suggest that there is a relationship between modularity and morphological disparity that involves shifts in rates of morphological evolution. The results of this third chapter also suggest that there are both similarities and differences in terms of patterns of morphological integration and modularity between the micro- and macroevolutionary scales. The patterns that were identified for actinopterygians as a whole could reflect a composite from several differing patterns of morphological integration intrinsic to a number of actinopterygian lineages.

An important conclusion stemming from the results of this doctoral thesis is that there is some correspondence between patterns of morphological integration and modularity at the micro- and macroevolutionary scales. Because the hypotheses of modularity tested were largely based on developmental data, this implies that a relationship exists between developmental, variational and evolutionary modularity, thus connecting processes that occur respectively within individuals, within populations and across species.

KEYWORDS: morphological disparity, modularity, fishes, median and paired fins, geometric morphometry.

INTRODUCTION GÉNÉRALE

Les groupes d'organismes diffèrent les uns des autres non seulement en termes de richesse spécifique, mais également en termes de différences morphologiques entre les espèces qui les composent. De plus, ces deux caractéristiques ne sont pas nécessairement liées : certaines lignées évolutives contiennent un grand nombre d'espèces aux morphologies relativement homogènes, alors que d'autres lignées évolutives contiennent peu d'espèces mais les différences morphologiques entre celles-ci sont maximisées par l'exploration de nouveaux horizons morphologiques (Gould 1989). Partant de cette observation, il importe de vérifier s'il existe des caractéristiques propres aux organismes vivants qui pourraient influencer la rapidité ou l'étendue de l'accumulation de différences morphologiques. Une propriété de l'organisation du vivant qui pourrait être à l'origine de ces différences est la modularité (West-Eberhard 2003). Le postulat de la modularité est que les organismes sont subdivisés en sous-unités fortement intégrées appelées des modules (Wagner 1996; Winther 2001; Klingenberg 2008). Puisque les modules sont des unités quasi-indépendantes au cours du développement et de l'évolution, ceux-ci peuvent suivre des trajectoires développementales ou évolutives distinctes du reste de l'organisme (Wagner 1996; Wagner and Altenberg 1996; Hansen 2003; Hansen et al. 2003; Hansen 2006). Pour cette raison, une organisation modulaire pourrait favoriser la capacité à évoluer des organismes (Bonner 1988; Raff 1996; Wagner 1996; Wagner and Altenberg 1996).

Cette thèse doctorale s'intéresse donc à la relation entre la disparité morphologique et l'organisation modulaire du vivant en utilisant les poissons comme organismes modèles. Dans cette introduction générale, les bases théoriques formant le cadre conceptuel des analyses qui ont été utilisées seront mises de l'avant. Ainsi, des définitions précises de ces termes potentiellement abstraits que sont la "disparité morphologique" et la "modularité" seront fournies, et les postulats reliant ces deux propriétés seront établis. Le choix des poissons comme organismes modèles sera

justifié, notamment dans l'optique où ils constituent un groupe à la fois diversifié et disparate, et pour lequel des hypothèses de modularité ont déjà été proposées dans la littérature scientifique. Finalement, une synthèse de ces différentes notions sera présentée dans le cadre de la problématique de recherche, et les objectifs spécifiques et les aspects méthodologiques des trois chapitres qui constituent cette thèse seront présentés.

Disparité morphologique

La disparité morphologique réfère aux différences morphologiques qui existent entre des taxons, alors que la diversité ou la richesse réfèrent plutôt au nombre de taxons qui composent un groupe (Gould 1989; Foote 1991, 1993a, 1997). Les clades diffèrent les uns des autres non seulement en termes de diversité spécifique, mais également en termes de disparité morphologique. Quoique cela puisse paraître contre-intuitif, les patrons en termes de diversité taxonomique et de disparité morphologique ne coïncident pas toujours (Foote 1991, 1992b, a, 1993b, 1994, 1995, 1997, 1999; Harmon et al. 2003) : certains clades possèdent une grande richesse spécifique mais avec peu de différences morphologiques entre les espèces, alors que d'autres ne contiennent que peu d'espèces qui sont morphologiquement toutes très différentes (Gould 1989). Non seulement les clades peuvent-ils être plus ou moins disparates, mais au sein même des organismes, les structures morphologiques diffèrent quant à leur capacité à produire de la disparité morphologique.

La disparification, soit l'accumulation de différences morphologiques entre des organismes ou entre des structures, peut être influencée par des différences quant aux propriétés variationnelles propres à certains groupes de traits (Vermeij 1973; Lewontin 1974; Raff 1996). Parmi ces propriétés, la labilité réfère à la capacité qu'ont certains traits à produire des changements phénotypiques rapides (certains termes sont définis dans le Lexique afin de ne pas alourdir inutilement le texte; ces termes sont soulignés

lorsqu'ils sont rencontrés pour la première fois), généralement en réponse à une modification dans l'environnement (Scheiner 1993; DeWitt and Scheiner 2004; Chown et al. 2008). Quoique la labilité soit généralement un concept qui s'applique à l'échelle des individus, certains auteurs parlent aussi de labilité évolutive dans le cadre de comparaisons entre des populations ou des espèces (Sánchez-Villagra et al. 2008; Jousselin et al. 2010; Donovan et al. 2014; Linde-Medina et al. 2016). La labilité évolutive de certains ensembles de traits pourrait contribuer à la production de disparité morphologique, notamment en permettant de nouvelles combinaisons de ces traits, favorisant ainsi l'émergence de nouveautés évolutives (Ogburn and Edwards 2009). Une autre propriété variationnelle s'appliquant à l'échelle macroévolutive est l'évolvabilité qui se définit comme étant la capacité à produire de la variation héritable et sur laquelle la sélection naturelle peut agir (Kirschner and Gerhart 1998; Eble 2005; Hansen 2006; Draghi and Wagner 2008; Hansen and Houle 2008). Ces propriétés variationnelles qui favorisent l'émergence de disparité morphologique pourraient à leur tour dépendre de l'organisation modulaire des êtres vivants.

Modularité

La modularité signifie que les organismes vivants (incluant aussi les formes fossiles) peuvent être subdivisés en sous-unités fortement intégrées que l'on appelle des modules (Wagner 1996; Winther 2001; Klingenberg 2008). La modularité est donc liée au concept d'intégration morphologique qui stipule que des traits qui sont associés en raison de contraintes développementales ou fonctionnelles devraient former des unités hautement cohésives (Olson and Miller 1958; Cheverud 1982; Zelditch 1987; Cheverud 1996a; Chernoff and Magwene 1999). Dans ce contexte, la modularité fait référence à la différence dans les niveaux d'intégration morphologique lorsque des traits appartenant à un module donné sont comparés avec des traits appartenant à d'autres modules distincts (Wagner 1996; Magwene 2001; Klingenberg 2008, 2009). Les auteurs ne s'entendent cependant pas tous sur ce que devraient être les attentes en

termes de patrons d'intégration morphologique pour des modules biologiques. Certains auteurs proposent une définition plus forte de la modularité focalisant sur la quasi-indépendance ou l'indépendance conditionnelle des modules (Magwene 2001; Hansen 2003; Hansen et al. 2003; Magwene 2009), alors que d'autres utilisent une définition plus inclusive selon laquelle les modules sont simplement plus fortement intégrés comparativement au reste de l'organisme (Bolker 2000, 2005; Eble 2005; Klingenberg 2008, 2009; Esteve-Altava 2016). Ceci n'est pas sans importance puisque ces visions conceptuelles divergentes de la modularité se reflètent dans des aspects analytiques des différentes méthodes statistiques disponibles pour évaluer des hypothèses de modularité. Dans le cadre de cette thèse doctorale, la définition forte de la modularité a été préconisée, celle-ci étant plus congruente avec les conséquences macroévolutives qui découlent d'une organisation modulaire. Les modules sont donc définis comme étant des unités hautement cohésives qui sont quasi-autonomes au cours du développement et/ou de l'évolution (Simon 1962; Magwene 2001; Müller 2007).

Il existe différents types de modules qui peuvent être catégorisés en fonction des processus dans lesquels ils sont impliqués. Les modules développementaux correspondent à des unités qui sont quasi-autonomes par rapport aux autres parties de l'organisme au cours du développement (Raff 1996; Wagner and Mezey 2004; Wagner et al. 2007). Les modules développementaux agissent à l'échelle des individus mais pour des raisons techniques, leur identification nécessite la reconstitution de séries de croissance à partir de données récoltées sur plusieurs individus. Les modules variationnels désignent des ensembles de traits phénotypiques qui sont fortement intégrés dans leurs patrons de variation, et quasi-indépendants relativement à d'autres ensembles de traits (Wagner and Mezey 2004; Eble 2005; Hendrikse et al. 2007; Wagner et al. 2007). Cette cohésion au sein des modules variationnels résulte des patrons d'expression de gènes pléiotropes au cours du développement (Cheverud 1996a; Wagner 1996; Wagner and Altenberg 1996; Wagner et al. 2007). Les modules variationnels sont étudiés en analysant les patrons de covariation ou de corrélation entre

des traits quantitatifs (Olson and Miller 1958; Cheverud 1982, 1996b; Magwene 2001; Márquez 2008). De plus, les modules variationnels sont analysés à l'échelle microévolutive, et donc au sein d'une population ou d'une espèce. Les modules évolutifs sont quant à eux constitués de traits qui co-évoluent (Cheverud 1982, 1996a; Brandon 1999). Les modules évolutifs sont donc étudiés à l'échelle macroévolutive, soit en analysant et en comparant les patrons de covariation entre différentes espèces. En raison de leur quasi-indépendance, les modules développementaux pourraient correspondre aussi à des modules variationnels et/ou à des modules évolutifs (Brandon 1999; Müller 2007). Hallgrímmson et al. (2009) ont cependant suggéré qu'une correspondance de un pour un entre les modules développementaux et variationnels ne devrait pas nécessairement être attendue puisque les modules variationnels résultent de l'action combinée de plusieurs processus développementaux au cours de l'ontogenèse, chacun de ceux-ci ayant des domaines d'expression spatiaux et temporels qui ne correspondent pas toujours. Ainsi, il est également possible que la correspondance ne soit pas toujours parfaite entre ces différentes catégories de modules.

La modularité est considérée comme une propriété importante pour l'évolvabilité des systèmes biologiques (Bonner 1988; Raff 1996; Wagner 1996; Wagner and Altenberg 1996). Ceci résulte du fait que les modules peuvent être individuellement optimisés sans pour autant affecter l'intégrité du reste de l'organisme (Wagner 1996; Wagner and Altenberg 1996; Hansen 2003; Hansen et al. 2003; Pavlicev and Hansen 2011). Cette capacité des modules à suivre des trajectoires évolutives quasi-indépendantes alors que les autres parties de l'organisme sont maintenues constantes est appelée l'évolvabilité conditionnelle (Hansen 2003; Hansen et al. 2003; Hansen 2006). La modularité peut aussi favoriser l'émergence de nouveautés évolutives. En effet, les modules peuvent être dupliqués, et par la suite diverger et/ou être co-optés pour accomplir d'autres fonctions (Raff 1996; Hansen 2006; Hendrikse et al. 2007). Ceci peut mener à l'apparition de structures répétées qui, si elles sont subséquemment découplées, peuvent suivre des trajectoires évolutives indépendantes (Raff 1996; Winther 2001;

Monteiro 2008). Il est suggéré que cette séquence d'évènements de duplication puis de découplage pourrait faciliter l'émergence d'innovations morphologiques et/ou anatomiques au cours de l'évolution (Riedl 1978; Weiss 1990; Raff 1996; Winther 2001; Kuratani 2009; Savriama et al. 2016). De ce fait, la modularité fournit un cadre conceptuel avantageux pour l'étude de l'origine de la disparité morphologique et fonctionnelle entre les organismes vivants (West-Eberhard 2003; Wagner et al. 2007).

Relation entre modularité et disparité morphologique

La disparité morphologique observée entre des taxons relève entre autres des propriétés variationnelles de certains ensembles de traits morphologiques. Une organisation modulaire influence les prédispositions variationnelles des organismes vivants et conséquemment, peut avoir une incidence sur le potentiel de disparification de différentes lignées évolutives (West-Eberhard 2003). Puisque les traits appartenant à un module donné peuvent évoluer d'une manière quasi-indépendante relativement au reste de l'organisme ou relativement à d'autres modules (Wagner 1996; Gerhart and Kirschner 2007), il en découle que la modularité peut faciliter l'émergence de disparité morphologique entre les populations ou entre les espèces (West-Eberhard 2003; Sanger et al. 2012).

L'une des hypothèses proposées pour expliquer cette influence de la modularité sur les processus de disparification est qu'une organisation modulaire pourrait avoir une incidence sur les taux d'évolution morphologique (Wagner 1996). Il est reconnu de longue date que des changements au niveau des taux d'évolution peuvent influencer l'accumulation de disparité morphologique entre des clades au cours de leurs diversifications évolutives (Foote 1997; Harmon et al. 2003; Ackerly and Nyffeler 2004; O'Meara et al. 2006; Sidlauskas 2007, 2008; Denton and Adams 2015). Certains auteurs ont proposé qu'une organisation plus modulaire (que ce soit en raison d'un plus grand nombre de modules ou d'une plus grande indépendance entre ceux-ci) pourrait

entraîner une augmentation des taux d'évolution morphologique (Claverie and Patek 2013). Une organisation modulaire pourrait également permettre aux différents modules d'avoir des taux d'évolution distincts (Denton and Adams 2015).

Cette hypothèse selon laquelle la modularité influencerait la disparité morphologique par l'entremise de changements dans les taux d'évolution ne fait cependant pas l'objet d'un consensus. Aguilar-Medrano et al. (2016) suggèrent plutôt l'inverse : une forte modularité pourrait être à l'origine de contraintes pour l'évolution morphologique, en plus de mener à une réduction des taux d'évolution morphologique. En appui à cette hypothèse, Goswami et al. (2014) ont observé, en analysant les patrons d'intégration morphologique du crâne d'un large éventail de mammifères, que les modules les plus fortement intégrés tendaient à être moins disparates, et inversement que les modules moins fortement intégrés étaient généralement plus disparates. De plus, malgré cette relation entre la force de l'intégration et les patrons de disparité morphologique, ces auteurs n'ont pu mettre en évidence une relation entre la disparité et les taux d'évolution morphologique, ni entre l'intégration morphologique et les taux d'évolution morphologique (Goswami et al. 2014). Goswami et al. (2009) ont proposé une autre hypothèse selon laquelle la modularité pourrait exercer une influence sur les niveaux de disparité morphologique en favorisant des changements hétérochroniques, soit des modifications dans la séquence, la durée ou la vitesse du développement de certaines parties de l'organisme au cours de l'ontogenèse (Gould 1977; Alberch et al. 1979; McKinney and McNamara 1991).

Il apparaît donc que les conséquences macroévolutives de la modularité sur la disparification et sur les taux d'évolution ne font pas l'unanimité au sein des auteurs. Goswami et al. (2009) proposent même que ce sont des changements dans les séquences ou dans les rythmes développementaux qui seraient à l'origine de la disparité morphologique observée, plutôt que des changements dans les taux d'évolution. Suivant ces constatations, il est évident qu'une clarification s'impose quant aux

relations qui existent entre la modularité, la disparité morphologique et les taux évolutifs.

Les poissons comme organismes modèles

Les poissons sont un groupe paraphylétique qui rassemble les représentants les plus basaux des vertébrés. C'est au cours de l'histoire évolutive des poissons que l'on voit apparaître de nombreuses structures-clés dans l'évolution des vertébrés, notamment le crâne, la colonne vertébrale, la mâchoire, et les membres pairs. De plus, les poissons sont le groupe de vertébrés le plus diversifié : les estimations actuelles en termes de richesse spécifique du groupe varient entre 31 000 et 32 000 espèces considérées comme valides (Eschmeyer et al. 2010; Nelson et al. 2016). De ce fait, les poissons constituent près de la moitié de la biodiversité spécifique au sein des vertébrés (~66 000 espèces). Les espèces actuelles et fossiles de poissons sont réparties dans un certain nombre de taxons (Figure 1) qu'il est important de définir brièvement puisque ceux-ci seront mentionnés dans les sections suivantes de l'introduction générale ainsi que dans les trois chapitres qui composent cette thèse doctorale.

Les poissons peuvent d'abord être subdivisés entre les agnathes, qui sont les poissons sans mâchoires, et les gnathostomes, qui sont donc les poissons possédant une mâchoire. Les agnathes constituent un assemblage paraphylétique qui ne sont plus représentés à l'époque actuelle que par deux ordres, soit les myxines (Myxiniformes; ~82 espèces actuelles et fossiles) et les lamproies (Petromyzontiformes; ~48 espèces actuelles et fossiles). Le registre fossile des agnathes est cependant nettement plus diversifié et inclut les conodontes, les ptéraspidomorphes, les anaspides, les thélodontes, les galéaspides, les pituriaspides et les ostéostracés (Long 1995; Janvier 1996b). Les conodontes comprennent ~1446 espèces (Sweet 1988; toutefois sachant que de nombreux taxons ont depuis été synonymisés, ce nombre représente vraisemblablement une surestimation) dont la vaste majorité ne sont connues que par

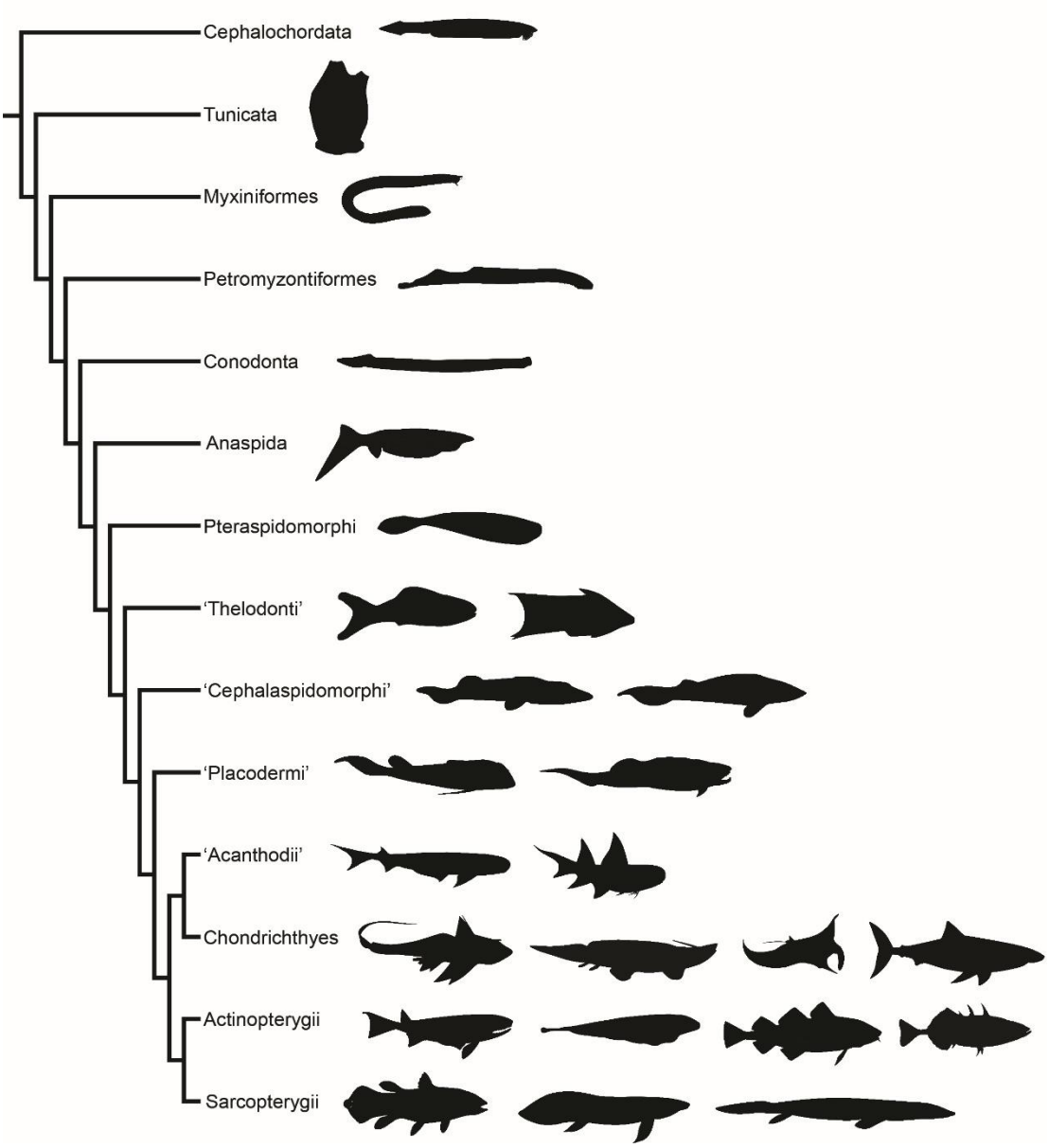

Figure 1 : Synthèse des relations phylogénétiques entre les groupes de poissons existants et fossiles illustrant l'importante disparité morphologique qui caractérise les poissons dans leur ensemble. Les groupes dont le nom est entre guillemets sont suspectés d'être paraphylétiques. La topologie résume les résultats de l'analyse phylogénétique présentée dans le chapitre premier de cette thèse.

des éléments fossilisés de l'appareil buccal (Sweet 1988; Dzik 1991; Aldridge and Smith 1993; Aldridge et al. 1995). Les ptéraspidomorphes, qui incluent les

hétérostracés, comprennent environ 300 espèces (A. Blieck, comm. pers.) et possèdent la tête et le tronc entièrement recouverts par une armure céphalothoracique massive. Les anaspides incluent environ 25 genres [mis à jour de Blom et al. (2002)] et sont caractérisés par la présence d'une nageoire caudale fortement hypocerque, ce qui se traduit en anatomie externe par un lobe inférieur plus développé comparativement au lobe supérieur. Les thélodontes, un groupe dont la monophylie est incertaine, comprennent ~132 espèces et possèdent des morphologies assez disparates : la majorité des taxons sont compressés dorso-ventralement mais les Furcacaudiformes sont plutôt trapus et, à l'inverse, compressés latéralement (Wilson and Caldwell 1993, 1998; Märss et al. 2007). Les céphalaspidomorphes sont un assemblage paraphylétique comprenant les galéaspides [~65 espèces (Zhu and Gai 2007)], les pituriaspides [seulement deux espèces connues (Young 1991)] et les ostéostracés [~214 espèces (Sansom 2009)], tous caractérisés par la présence d'un bouclier céphalothoracique recouvrant la tête et la région branchiale. De plus, les ostéostracés possèdent des nageoires paires qui sont généralement considérées comme étant homologues aux nageoires pectorales des gnathostomes (Kiaer 1924; Stensiö 1927, 1932, 1964; Maisey 1986; Forey and Janvier 1993, 1994; Forey 1995; Janvier and Arsenault 1996; Johanson 2002; Janvier et al. 2004a; Janvier 2007; Wilson et al. 2007; Sansom 2009).

Les gnathostomes sont nettement plus diversifiés que les agnathes, notamment en termes de représentants actuels. Les gnathostomes comprennent deux groupes exclusivement fossiles, les placodermes et les acanthodiens, et deux groupes comportant des représentants actuels, les chondrichthyens et les ostéichthyens. Les placodermes, qui incluent environ 335 genres dont la majorité sont monospécifiques, sont caractérisés par une région céphalothoracique recouverte par une série de plaques osseuses (Denison 1978; Young 2010). Les acanthodiens, qui incluent environ 100 genres, sont caractérisés par la présence d'épines insérées à l'avant des nageoires paires et impaires, à l'exception de la nageoire caudale (Watson 1937; Denison 1979). Les chondrichthyens, qui comprennent les requins, les raies et les chimères, incluent ~1251

espèces existantes et ~3000 espèces fossiles (Compagno et al. 2005; Klimley 2013). Les chondrichthyens sont caractérisés par la présence d'un squelette cartilagineux ainsi que par une modification d'une partie des nageoires pelviennes chez les mâles afin de servir d'organes d'intromission lors de l'accouplement (Schaeffer and Williams 1977; Maisey 1986; Grogan et al. 2012). Les ostéichthyens sont quant à eux caractérisés par la présence d'un squelette osseux. Les ostéichthyens comprennent les actinoptérygiens, le groupe de loin le plus diversifié au sein des vertébrés, et les sarcoptérygiens qui incluent aussi l'ensemble des tétrapodes. Les actinoptérygiens, qui possèdent des nageoires supportées par des rayons, ont connu un succès écologique et évolutif remarquable (Lauder and Liem 1983) et incluent plus de 30 500 espèces (Nelson et al. 2016). Non seulement les actinoptérygiens sont-ils extrêmement diversifiés, mais ils présentent en plus une impressionnante disparité morphologique dans de nombreux aspects de leur anatomie. Les sarcoptérygiens sont caractérisés par des nageoires paires qui sont généralement insérées sur un lobe charnu et qui sont supportées par un endosquelette monobasal (Cloutier and Ahlberg 1996; Janvier 1996b). Excluant les tétrapodes, les sarcoptérygiens ne comprennent que huit espèces existantes mais possèdent un registre fossile comparativement bien plus riche incluant ~190 genres (mis à jour de Cloutier and Ahlberg 1996).

Les nageoires chez les poissons : définitions opérationnelles

Il est reconnu de longue date qu'une caractéristique généralisée chez les poissons constitue la présence de nageoires (Aristotle et al. 1878; Aristotle and Barthélémy-Saint-Hilaire 1883). Il peut donc paraître surprenant qu'une définition anatomique et fonctionnelle précise de ce qui constitue une nageoire soit pratiquement inexistante dans la littérature récente. Ceci relève sans doute du fait qu'au cours de l'histoire évolutive des poissons, ces appendices locomoteurs ont fréquemment été modifiés, parfois même co-optés afin d'accomplir de nouvelles fonctions, si bien que l'élaboration d'une définition universelle du terme devient une tâche fastidieuse. Dans

Tableau 1 : Terminologie et définitions des nageoires considérées dans le cadre des analyses.

Nageoire	Définition	Autres appelations rencontrées dans la littérature
Nageoire médiane ventrale	Nageoire impaire ventrale insérée soit à l'avant ou à l'arrière de la nageoire anale lorsque celle-ci est présente.	*Preanal fin*; *ventral adipose fin*
Nageoires paires ventro-latérales	Nageoires généralement allongées insérés ventro-latéralement le long du tronc.	*Ventrolateral fins* ou *finfolds*; *intermediate spines*; *prepelvic spines*
Nageoires pectorales	Nageoires paires insérées au niveau du thorax près des branchies et à base étroite.	*Suprabranchial fins*; *paired* ou *pectoral flaps*; *pectoral swimming appendages*
Nageoires pelviennes	Nageoires paires insérées ventralement et toujours situées antérieurement à l'anus.	*Ventral fins*
Nageoire(s) dorsale(s)	Nageoire(s) insérée(s) le long de l'axe médian dorsal, entre la tête et la nageoire caudale.	
Nageoire(s) anale(s)	Nageoire(s) insérée(s) le long de l'axe médian dorsal, entre l'anus et la nageoire caudale.	
Nageoire adipeuse	Petite nageoire sans rayons située entre les nageoires dorsale et caudale et présente chez certains eutéléostéens.	*Fatty fin*; *dorsal organ*; *dorsal filament*
Nageoire caudale	Nageoire située à l'extrémité postérieure de la queue.	*Tail fin*

le cas présent, les nageoires ont été définies comme étant des structures qui projettent à partir du corps, composées d'une membrane supportée ou non par des éléments squelettiques, et qui sont généralement utilisées à des fins de locomotion (voir Annexe

A). Ceci étant dit, certains poissons possèdent des membranes sans support squelettique (p. ex. certaines nageoires adipeuses) ou des éléments de support squelettique sans membrane [p. ex. la série d'épines chez les épinoches (*Gasterosteus* sp.)] et ces structures devraient néanmoins être considérées comme étant des nageoires (Lacépède 1798; Lacépède et al. 1853).

De plus, considérant l'étendue de la disparité morphologique dans l'anatomie et la morphologie des nageoires entre les groupes de poissons, et considérant les divergences d'opinions quant aux relations d'homologie entre certaines nageoires, notamment pour les taxons fossiles (voir Annexe B), il a été nécessaire dans le cadre de ce projet d'élaborer une série de critères opérationnels dans l'identification de celles-ci. Les critères qui sont généralement utilisés pour reconnaître des structures homologues sont : (1) la similarité (correspondance topographique et de transformation ontogénétique), (2) la conjonction (ou singularité anatomique), et (3) la congruence (congruence phylogénétique avec d'autres homologies) (Patterson 1982, 1988). Dans le cas présent, le critère de similarité topographique a été principalement utilisé, mais des critères structuraux et développementaux ont également été considérés dans les cas où la topographie était insuffisante pour l'identification d'une nageoire (Tableau 1; Figure 2).

Disparité morphologique dans la configuration des nageoires

Les poissons sont non seulement extrêmement diversifiés mais ils démontrent également une impressionnante disparité morphologique. Or, il est reconnu de longue date (Goüan 1770; Lacépède 1798; Cuvier and Valenciennes 1828; Aristotle et al. 1878) qu'une partie importante de cette disparité morphologique relève de l'organisation des nageoires, que ce soit en raison de différences entre les taxons concernant le nombre de nageoires présentes, leur taille, leur forme, leur type de support squelettique, ou leur position relative sur le corps du poisson. En effet, de nombreuses divergences écologiques, notamment au niveau des modes de locomotion

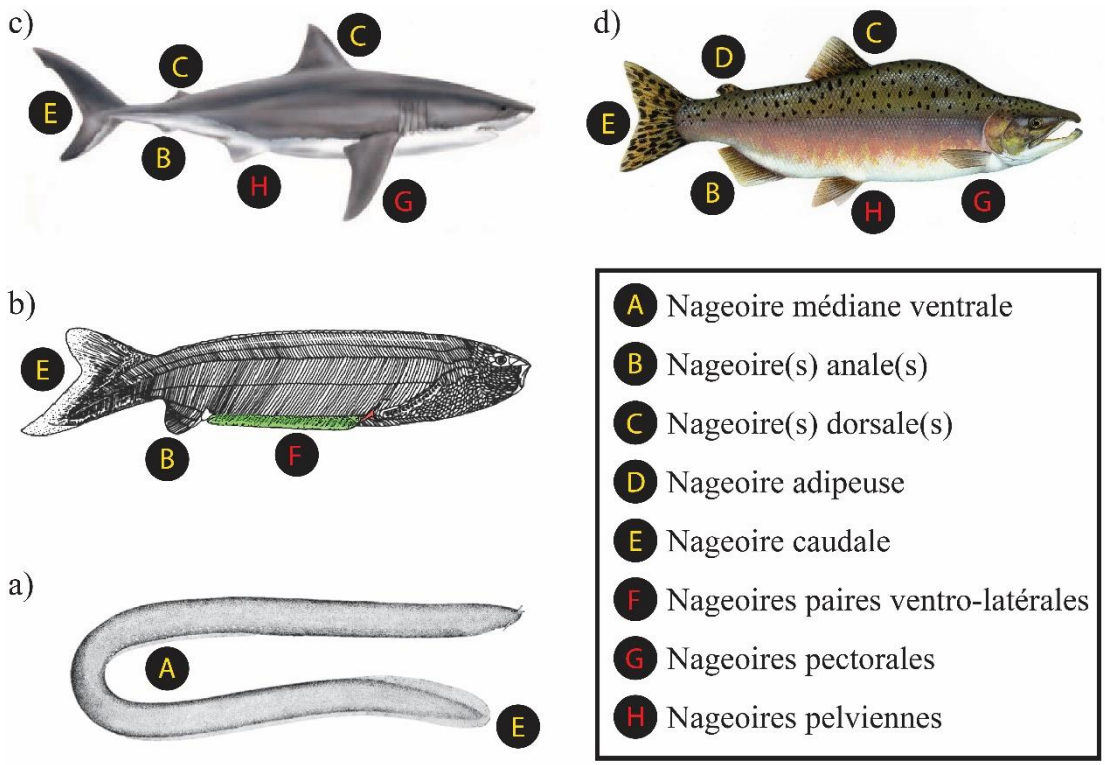

Figure 2 : Représentations schématiques de quelques agnathes et gnathostomes afin d'illustrer la diversité des types de nageoires au sein des poissons. Les pastilles avec un lettrage jaune identifient des nageoires médianes alors que celles avec un lettrage rouge identifient des nageoires paires. Les illustrations représentent : (a) une myxine, (b) un anaspide, (c) un chondrichthyen, et (d) un actinoptérygien (liens webs des illustrations utilisées fournis après la liste de références bibliographiques).

ou des stratégies d'alimentation, sont associés à des modifications dans la configuration des nageoires (Webb 1982; Lauder and Liem 1983; Webb 1984; Lauder and Drucker 2004; Shubin and Davis 2004).

Une partie de cette disparité morphologique dans la configuration des nageoires chez les poissons relève de la présence ou de l'absence de certains de ces appendices locomoteurs. Des exemples de perte sont connus pour chacune des nageoires médianes et paires. Même la nageoire caudale qui est le principal moyen de propulsion chez la majorité des poissons peut occasionnellement être perdue, un exemple bien connu étant

le poisson-lune (*Mola mola*) (Johnson and Britz 2005). Les nageoires pelviennes semblent être particulièrement évolutivement labiles en termes de présence/absence. De nombreux caractères liés aux nageoires ou à la ceinture pelvienne sont apparus ou ont été perdus à plusieurs reprises au cours de l'évolution des actinoptérygiens. Par exemple, la perte des nageoires pelviennes serait survenue lors d'au moins 80 évènements distincts chez les téléostéens (Yamanoue et al. 2010). De plus, au cours de la transition des nageoires paires des poissons sarcoptérygiens vers les membres pairs des tétrapodes, certains auteurs ont noté un patron distinctif d'indépendance partielle dans les changements affectant les appendices pectoraux et pelviens (Coates and Cohn 1998, 1999; Coates et al. 2002). Une autre tendance dans la disparification des configurations de nageoires constitue l'addition de nouvelles nageoires, soit par la duplication (ou même la triplication) de nageoires préexistantes, comme chez la morue (*Gadus morhua*) qui présente trois nageoires dorsales séparées, ou par l'addition de nageoires constituant des nouveautés évolutives, comme par exemple la nageoire adipeuse chez de nombreux eutéléostéens (Stewart et al. 2014). Les nageoires paires et médianes peuvent également varier quant à leur étendue ainsi que leur position relative sur le corps du poisson.

Malgré ces nombreux aspects favorisant la disparification dans l'organisation des nageoires chez les poissons, certaines tendances évolutives peuvent néanmoins être mises de l'avant. Ainsi, la majoprité des actinoptérygiens basaux possèdent une seule nageoire dorsale supportée par des rayons mous, alors que chez les acanthoptérygiens, une seconde nageoire dorsale est souvent présente, celle-ci étant insérée plus antérieurement et étant supportée par des épines (Lauder and Liem 1983; Drucker and Lauder 2001; Lauder et al. 2002). De plus, les nageoires dorsale et anale tendent à être positionnées symétriquement le long de l'axe antéro-postérieur chez les actinoptérygiens basaux (Mabee et al. 2002) ainsi que chez de nombreux acanthoptérygiens (Lauder and Drucker 2004). Comparativement, chez les téléostéens basaux, les nageoires dorsale et anale sont décalées l'une de l'autre le long de l'axe

antéro-postérieur (Lauder and Drucker 2004). De plus, chez les téléostéens basaux, l'extrémité postérieure de la nageoire dorsale est située environ au centre de l'axe antéro-postérieur du corps, alors que chez les téléostéens plus dérivés, elle se situe plus postérieurement au-dessus du pédoncule caudal (Lauder and Drucker 2004). Les nageoires pectorales sont positionnées ventro-latéralement avec un angle d'insertion horizontal chez les actinoptérygiens basaux et la majorité des chondrichthyens, alors que chez les actinoptérygiens plus avancés, elles sont positionnées latéralement avec un angle d'insertion vertical (Greenwood et al. 1966; Rosen 1982; Lauder and Liem 1983; Drucker and Lauder 2002; Lauder and Drucker 2004). Les nageoires pelviennes, quant à elles, sont insérées ventralement et approximativement au centre de l'axe antéro-postérieur du corps chez les actinoptérygiens basaux, alors qu'elles se déplacent vers l'avant et se rapprochent du centre de masse chez les actinoptérygiens plus dérivés (Greenwood et al. 1966; Rosen 1982; Lauder and Liem 1983; Lauder and Drucker 2004; Yamanoue et al. 2010).

Apparition séquentielle des nageoires

La séquence évolutive représentant l'apparition successive des différentes nageoires chez les poissons n'a pas encore été entièrement résolue, quoiqu'une excellente synthèse de ce qui est connu à ce sujet au niveau moléculaire ait été publiée par Freitas et al. (2014). La majorité des nageoires (à l'exception des nageoires pelviennes et adipeuse) apparaissent tôt au cours de l'histoire évolutive des poissons, soit au sein des agnathes. Tel que mentionné précédemment, les représentants actuels des agnathes se limitent aux myxines et aux lamproies alors que leur registre fossile est comparativement nettement plus diversifié et considérablement plus disparate. C'est donc du côté du registre fossile qu'il faut se tourner afin d'élucider la disparification progressive des patrons de configuration des nageoires. Celui-ci démontre sans ambiguïté que l'apparition des nageoires médianes précède celle des nageoires paires (Shu et al. 1999; Shu et al. 2003a; Zhang and Hou 2004). L'interprétation de la suite

de cette histoire évolutive des appendices locomoteurs chez les poissons est cependant plus problématique. Deux éléments viennent complexifier la résolution de cette question fondamentale : (1) les phylogénies des vertébrés basaux (p. ex. Forey 1995; Janvier 1996a; Donoghue et al. 2000; Donoghue and Smith 2001; Sansom et al. 2010; Turner et al. 2010; Keating and Donoghue 2016) et des gnathostomes basaux (p. ex. Brazeau 2009; Davis et al. 2012; Zhu et al. 2013; Dupret et al. 2014; Giles et al. 2015c; Long et al. 2015; Burrow et al. 2016; Qiao et al. 2016) n'ont pas encore fait l'objet d'un consensus, (2) et les relations d'homologie entre les nageoires présentes au sein des différents groupes d'agnathes et celles des gnathostomes ne font également pas l'objet d'un consensus (Johanson 2010; voir Annexe B).

Apparition des nageoires médianes

Malgré l'absence de consensus, il n'en demeure pas moins qu'il est maintenant bien établi que les nageoires ont d'abord fait leur apparition dans l'axe médian du corps. Une nageoire caudale est présente chez la majorité des agnathes pour lesquels cette région du corps est suffisamment conservée, à l'exception d'une myxine fossile, *Gilpichthys greenei*, et d'une lamproie fossile, *Pipiscius zangerli* (Bardack and Richardson 1977) datant tous deux du Carbonifère supérieur. Il est cependant possible que l'absence de nageoire caudale chez ces formes représente un caractère larvaire ou encore que cela résulte d'un artéfact taphonomique, soit à une préservation incomplète de cette région chez ces spécimens (Bardack and Richardson 1977).

Quant aux autres nageoires médianes, les plus vieux vertébrés connus, datant du Cambrien inférieur il y a environ 535 millions d'années, possédaient des nageoires médianes dorsales et ventrales bien développées, mais pas de nageoires paires (Shu et al. 1999; Shu et al. 2003a; Zhang and Hou 2004). En fonction du critère topographique, ces nageoires médianes pourraient correspondre à des nageoires dorsales et préanales. Parmi les agnathes, des nageoires dorsales sont également présentes chez plusieurs

lamproies, anaspides, thélodontes et ostéostracés. Quant à la nageoire préanale, celle-ci est une caractéristique partagée par la majorité des myxines actuelles. Cependant, en raison de leurs étendues considérables le long de l'axe antéro-postérieur du corps, les nageoires médianes des premiers vertébrés rappellent aussi le repli natatoire médian présent pendant l'ontogenèse chez les poissons plus dérivés (van den Boogaart et al. 2012), ou encore les replis natatoires dorsaux et ventraux des céphalochordés (Andrews 1893; Kirkaldy 1895; Bigelow and Farfante 1948; Holland and Holland 1991).

Considérant la définition adoptée selon laquelle une nageoire anale est insérée postérieurement à l'anus, une nageoire anale est présente chez les anaspides, certains thélodontes ainsi que chez la majorité des gnathostomes. Parmi les anaspides, *Euphanerops longaevus*, datant du Dévonien supérieur, présente une condition particulière. En effet, *Euphanerops* était considéré comme possédant une nageoire anale (Stensiö 1939; Arsenault and Janvier 1991; Janvier and Arsenault 2007) mais une nouvelle analyse plus détaillée du matériel a révélé que cette nageoire anale serait en réalité une structure paire (Sansom et al. 2013). La présence d'une nageoire anale paire est une condition unique au sein des vertébrés. Chez les lamproies, la nageoire anale est normalement absente (Renaud 2011). Cependant, une nageoire anale a également été décrite pour certaines lamproies fossiles (Bardack and Zangerl 1968; Janvier and Lund 1983). Une nageoire anale a aussi occasionnellement été observée chez des lamproies actuelles (Vladykov 1973; Vladykov and Kott 1980), ce qui est considéré comme un cas d'atavisme (Janvier 1996a, 2007, 2008).

Duplications de la nageoire dorsale

Parmi les agnathes, la majorité des lamproies actuelles, à l'exception des représentants du genre *Ichthyomyzon*, possèdent deux nageoires dorsales (Renaud 2011). Certains ostéostracés, *Ateleaspis tessellata*, *Acerapis robustus* et *Hirella gracilis* datant du Silurien moyen et supérieur, sont également caractérisés par la présence de deux

nageoires dorsales (Heintz 1939; Ritchie 1967); ces derniers sont résolus comme occupant une position basale au sein de ce groupe (Janvier 1985a, c; Blieck and Janvier 1991; Janvier 1996b; Sansom 2008, 2009). Ces observations semblent indiquer que des duplications des nageoires dorsales se seraient produites à plus d'une reprise au sein des agnathes.

Quant aux gnathostomes, il est généralement considéré que la condition plésiomorphe pour ce groupe constitue la présence de deux nageoires dorsales (Janvier 1996b; Lund and Grogan 1997; Hanke 2002; Maisey 2009). Les groupes les plus basaux de placodermes pour lesquels le matériel permet d'interpréter ce caractère possèdent une seule nageoire dorsale. Cependant les représentants des stensioellides et des brindabellaspides, deux groupes qui sont habituellement interprétés et/ou résolus comme étant parmi les placodermes les plus basaux (Denison 1978; Goujet and Young 1995; Brazeau and de Winter 2015; Giles et al. 2015c; Lu et al. 2016a; Qiao et al. 2016), ne permettent pas l'interprétation du nombre de nageoires dorsales présentes en raison de la préservation incomplète du matériel postcrânien. Chez les acanthodiens, les représentants de trois des quatre ordres, soit les Ischnacanthiformes, Climatiiformes et Diplacanthiformes, possèdent tous deux nageoires dorsales. Le quatrième ordre d'acanthodiens, les Acanthodiformes, ont une seule nageoire dorsale mais ceci est considéré comme étant une condition apomorphe de ce groupe (Denison 1979; Hanke 2002; Burrow 2004). Chez les chondrichthyens, la condition plésiomorphe quant au nombre de nageoires dorsales est difficile à déterminer (Lund 1985). En effet, la phylogénie d'une partie des chondrichthyens basaux n'a pas encore été entièrement résolue (p. ex. Lund and Grogan 1997; Grogan and Lund 2008; Lund et al. 2014). De plus, l'état de préservation du matériel postcrânien des élasmobranches les plus primitifs ne permet pas d'interpréter la présence ou l'absence d'une nageoire dorsale postérieure (Young 1982; Miller et al. 2003).

Chez les ostéichthyens, Schultze (1986) a proposé que deux nageoires dorsales constituaient la condition plésiomorphe du groupe. *Guiyu oneiros*, un ostéichthyen basal du Silurien supérieur (Qiao et al. 2016) dont une partie de l'anatomie postcrânienne est connue, a initialement été interprété avec une seule nageoire dorsale (Zhu et al. 2009) mais une reconstruction artistique plus récente suggère que deux nageoires dorsales étaient présentes (Zhu et al. 2012a). *Dialipina salgueiroensis*, du Dévonien inférieur, qui est résolu tantôt comme un ostéichthyen basal (Friedman 2007; Brazeau 2009; Davis et al. 2012; Dupret et al. 2014; Brazeau and de Winter 2015; Giles et al. 2015c; Burrow et al. 2016; Lu et al. 2016a) et tantôt comme le plus primitif des actinoptérygiens (Taverne 1997; Schultze and Cumbaa 2001; Zhu and Schultze 2001; Cloutier and Arratia 2004; Zhu et al. 2006; Zhu et al. 2009; Giles et al. 2015b; Long et al. 2015), possède aussi deux nageoires dorsales (Schultze and Cumbaa 2001). La majorité des autres actinoptérygiens basaux possèdent cependant une seule nageoire dorsale ce qui suggère que la condition plésiomorphe pour les actinoptérygiens aurait été la présence de deux nageoires dorsales, mais que la nageoire dorsale antérieure a été perdue tôt au cours de l'histoire évolutive de ce groupe (Schultze and Cumbaa 2001; Cloutier and Arratia 2004). En effet, chez les actinoptérygiens non-téléostéens, outre *Dialipina*, la présence de deux nageoires dorsales n'est connue que pour le genre *Placidichthys* (Ionoscopiformes) (Brito 2000; Brito and Alvarado-Ortega 2008) ainsi que pour *Agoultichthys chattertoni* (Macrosemiiformes) (Murray and Wilson 2009). Phylogénétiquement, la seconde nageoire dorsale est un aspect hautement conservé au sein des gnathostomes alors que la co-option ou la perte de la première dorsale est un caractère dérivé fréquemment répété (Maisey, 2009).

Apparition des nageoires paires

Les premières nageoires paires seraient apparues quant à elles au sein des anaspides (Coates and Cohn 1998, 1999). Cependant, l'homologie entre les nageoires paires des anaspides et les nageoires pectorales et pelviennes des gnathostomes est incertaine

(Wilson et al. 2007). Les vertébrés les plus basaux qui possèdent des nageoires paires supportées par des structures endosquelettiques et dont les mouvements sont contrôlés par une musculature associée sont les ostéostracés (Forey 1995; Coates and Cohn 1998, 1999; Coates 2003). Ces nageoires paires chez les ostéostracés sont considérées par la plupart des auteurs comme étant homologues aux nageoires pectorales des gnathostomes (Kiaer 1924; Stensiö 1927, 1932, 1964; Maisey 1986; Forey and Janvier 1993, 1994; Forey 1995; Janvier and Arsenault 1996; Johanson 2002; Janvier et al. 2004a; Janvier 2007; Wilson et al. 2007; Sansom 2009).

Parmi les hypothèses concernant l'histoire évolutive des nageoires paires, l'une des possibilités est que celles-ci résultent de condensations de replis pairs cutanés (Balfour 1876; Thacher 1877; Balfour 1878; Mivart 1879; Balfour 1881; Goodrich 1906). Ce sont des études développementales et comparatives, utilisant entre autres des chondrichthyens comme organismes modèles, qui ont amené Balfour (1876), Thacher (1877) et Mivart (1879) à conclure indépendamment l'un de l'autre que les nageoires paires, tout comme les nageoires impaires, ont évolué à partir d'un repli natatoire continu. L'un des principaux arguments en faveur de cette hypothèse du repli natatoire latéral est que les similitudes anatomiques et moléculaires remarquables qui existent au cours du développement entre les nageoires paires et médianes ne peuvent être expliquées que si elles partagent une origine commune (Osburn 1907; Yonei-Tamura et al. 2008). De plus, il a été démontré que chez les vertébrés, la formation de membres additionnels pouvait être induite au niveau des flancs, dans la région située entre les membres antérieurs et postérieurs (Cohn et al. 1995; Isaac et al. 1998; Tanaka et al. 2000; Tamura et al. 2001; Tanaka et al. 2002). Ces résultats concordent avec l'hypothèse du repli natatoire latéral puisqu'ils démontrent que l'ensemble de la région ventro-latérale constitue une zone de compétence pour le développement de membres additionnels (Yonei-Tamura et al. 2008). L'hypothèse de l'archiptérygium de Gegenbaur représente une alternative à l'hypothèse du repli natatoire latéral et propose plutôt que les nageoires paires dérivent d'arcs branchiaux modifiés (Gegenbaur 1876).

La vraisemblance de cette hypothèse est plus difficile à évaluer considérant l'absence de stades intermédiaires dans le registre fossile illustrant la séquence de transformations entre les arcs branchiaux et les nageoires paires (Osburn 1907). Cependant, récemment, des similitudes moléculaires entre le développement des arcs branchiaux et des nageoires paires ont été mises de l'avant et viennent donc supporter l'hypothèse de l'archiptérygium de Gegenbaur (Gillis et al. 2009).

Les deux hypothèses précédemment mentionnées concernent l'apparition des nageoires paires mais sans mentionner explicitement si les nageoires pectorales ou pelviennes sont apparues en premier. L'hypothèse la plus commune est que l'apparition des nageoires pectorales précède celle des nageoires pelviennes (Coates 1993; Forey and Janvier 1993; Coates 1994; Shubin et al. 1997; Coates and Cohn 1998, 1999; Ruvinsky and Gibson-Brown 2000). L'hypothèse alternative est bien entendu que les nageoires pelviennes sont apparues en premier (Tabin and Laufer 1993; Wilson et al. 2007). La majorité des auteurs considèrent que des nageoires pectorales homologues à celles des gnathostomes sont présentes chez les ostéostracés (Kiaer 1924; Stensiö 1927, 1932, 1964; Maisey 1986; Forey and Janvier 1993, 1994; Forey 1995; Janvier and Arsenault 1996; Johanson 2002; Janvier et al. 2004a; Janvier 2007; Wilson et al. 2007; Sansom 2009) et que de véritables nageoires pelviennes supportées par une ceinture pelvienne sont présentes chez la majorité des placodermes (Janvier 1996b; Shubin et al. 1997; Zhu et al. 2012b; Sansom et al. 2013; Trinajstic et al. 2014). La différence entre les deux scénarios évolutifs proposés relève en partie d'interprétations divergentes quant aux relations d'homologie proposées pour les nageoires paires de certains groupes d'agnathes. Wilson et al. (2007) suggèrent notamment que les nageoires ventro-latérales, présentes entre autres chez plusieurs anaspides, seraient homologues aux nageoires pelviennes des gnathostomes. En fonction de cette interprétation, les nageoires pelviennes seraient donc apparues en premier. Une dernière hypothèse est que des appendices pairs auraient pu apparaître à plusieurs reprises indépendamment au sein des vertébrés (p. ex. Sansom et al. 2013; Trinajstic et

al. 2014), complexifiant encore davantage l'interprétation des homologies. L'apparition indépendante d'appendices pairs ne serait pas surprenante considérant l'étendue de la zone de compétence au niveau des flancs pour le développement des membres (Yonei-Tamura et al. 2008).

Les données développementales et moléculaires semblent supporter davantage l'hypothèse selon laquelle les nageoires pectorales seraient apparues avant les nageoires pelviennes. En effet, l'observation de séquences ontogénétiques ont permis de démontrer que les nageoires pectorales se développent avant les nageoires pelviennes chez des chondrichthyens (p. ex. Ballard et al. 1993; Didier et al. 1998), des actinoptérygiens (p. ex. Grandel and Schulte-Merker 1998; Faustino and Power 1999) et des sarcoptérygiens (p. ex. Joss and Longhurst 2001). Des données développementales suggèrent aussi que le mésoderme des lames latérales (*lateral plate mesoderm*) se serait subdivisé en couches somatique et splanchnique séquentiellement de l'avant vers l'arrière au cours de l'évolution des chordés (Tanaka and Onimaru 2012). Or, les bourgeons des membres se forment à même le mésoderme latéral somatique (Tanaka and Onimaru 2012; Tanaka 2013) et donc la capacité à former des membres pairs aurait était contrainte de suivre cette même trajectoire évolutive de l'avant vers l'arrière. D'un point de vue moléculaire, deux des gènes impliqués dans la spécification de l'identité et le positionnement des membres pairs sont *Tbx5* pour les nageoires pectorales et *Tbx4* pour les nageoires pelviennes (Gibson-Brown et al. 1996; Isaac et al. 1998; Tamura et al. 2001). Une hypothèse est que ces gènes résultent de la duplication d'un gène ancestral : *Tbx4/5* (Agulnik et al. 1996; Ruvinsky and Gibson-Brown 2000; Tanaka et al. 2002). Selon les scénarios envisagés, des nageoires se seraient d'abord développées dans une position topologique correspondant aux nageoires pectorales, puis la duplication et l'évolution subséquente du gène *Tbx4/5* aurait permis aux gènes *Tbx5* et *Tbx4* de définir l'identité des nageoires pectorales et des nageoires pelviennes respectivement (Ruvinsky and Gibson-Brown 2000).

Modularité des nageoires

Une organisation modulaire des nageoires pourrait fournir un cadre conceptuel avantageux pour expliquer à la fois la disparification dans la configuration des nageoires observée au sein des poissons, mais également pour interpréter la séquence évolutive d'apparition de ces appendices locomoteurs. En effet, la modularité des nageoires pourrait influencer l'accumulation de disparité morphologique en permettant à certaines d'entre elles de suivre des trajectoires évolutives indépendantes. De plus, la duplication de modules préexistants de nageoires pourrait fournir un mécanisme afin d'expliquer l'émergence de nouvelles nageoires au cours de l'évolution. Des hypothèses de modularité des nageoires ont d'ailleurs déjà été suggérées, quoique pas toujours de manière explicite, dans le contexte de l'évolution des nageoires paires chez les vertébrés basaux (Freitas et al. 2006; Freitas et al. 2014), des nageoires pectorales et pelviennes chez les gnathostomes (Shubin et al. 1997), du complexe de la "brosse-épineuse" (*spine-brush complex*) de la première nageoire dorsale chez les requins symmoriiformes (Maisey 2009), de la nageoire adipeuse chez les eutéléostéens (Stewart and Hale 2013; Stewart et al. 2014; Stewart 2015), et finalement de la première nageoire dorsale épineuse chez les actinoptérygiens acanthomorphes (Mabee et al. 2002).

Hypothèses de modularité des nageoires médianes

Un certain nombre de modules ont déjà été proposés en ce qui concerne les nageoires chez les poissons. En commençant avec les hypothèses qui concernent les nageoires médianes (Figure 3), Mabee et al. (2002) ont suggéré que la nageoire dorsale et la nageoire anale partagent un module de positionnement. Cette hypothèse relève de l'observation que chez les actinoptérygiens basaux, ces deux nageoires tendent à présenter des positions symétriques relativement à l'axe antéro-postérieur du corps. Des modules de positionnement pourraient aussi être impliqués dans le développement

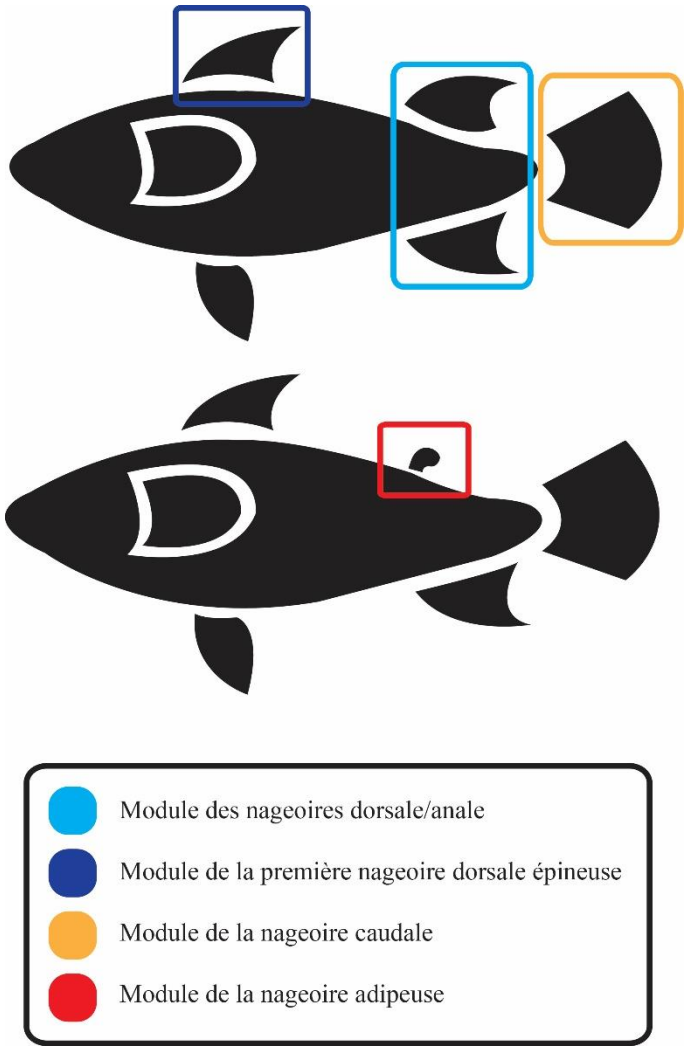

Figure 3 : Hypothèses de modularité suggérées pour les nageoires médianes.

des nageoires médianes chez les chondrichthyens : chez la petite roussette (*Scyliorhinus canicula*), l'identité et la position des nageoires dorsales et anale sont spécifiées par des patrons d'expression de gènes similaires (Freitas et al. 2006), suggérant l'implication de modules développementaux partagés entre ces deux nageoires. À l'origine, le module de positionnement des nageoires dorsale et anale aurait été couplé à un second module définissant les patrons de formation des éléments

squelettiques de support de ces deux nageoires (Mabee et al. 2002). À l'appui de cette seconde hypothèse, il a été rapporté que chez le poisson zèbre (*Danio rerio*), le patron bidirectionnel de formation des radiaux est similaire entre les nageoires dorsale et anale et est sous le contrôle des même patrons d'expression génique (Crotwell et al. 2001; Crotwell et al. 2004). Un autre module a été proposé pour les nageoires dorsale et anale régissant cette fois la coordination dans les séquences développementales entre les éléments de support endo- et exosquelettiques de ces nageoires (Mabee et al. 2002). Il importe de mentionner que ces deux modules régissant les patrons de formation des éléments de support squelettique des nageoires dorsale et anale ne semblent pas être exclusifs aux actinoptérygiens existants. En effet, des similarités dans le développement des éléments de support squelettique de ces deux nageoires ont également été observées chez des actinoptérygiens et sarcoptérygiens fossiles, suggérant que ces modules pourraient avoir été hérités d'un ancêtre commun à l'ensemble des ostéichthyens (Charest and Cloutier 2008; Cloutier 2010). Un module a également été suggéré au niveau de la nageoire caudale basé sur le conservatisme de séquences développementales et la similarité dans les réponses en termes de plasticité phénotypique chez l'omble chevalier (*Salvelinus alpinus*) (Grünbaum et al. 2012).

Selon Mabee et al. (2002), la nageoire dorsale antérieure que l'on retrouve chez de nombreux acanthoptérygiens constitue un nouveau module, résultant de la duplication puis de la divergence (les rayons sont remplacés par des épines) du module de la nageoire dorsale postérieure. Les acanthoptérygiens ne sont cependant pas le seul groupe de poissons caractérisé par la présence de plus d'une nageoire dorsale. Chez la majorité des gnathostomes, lorsque deux nageoires dorsales sont présentes, leurs morphologies sont similaires, ce qui suggère que leurs modules respectifs suivent rarement des trajectoires évolutives divergentes (Maisey, 2009). À l'inverse, lorsque les deux nageoires dorsales exhibent des morphologies distinctes, la nageoire dorsale postérieure est habituellement hautement conservée alors que c'est la nageoire dorsale antérieure qui est modifiée, comme par exemple chez les chimères, les actinistiens et

les requins symmoriiformes (Maisey 2009). Ceci serait vraisemblablement lié à des cas de co-option impliquant des transformations à la fois morphologiques et fonctionnelles d'un module préexistant de la première nageoire dorsale, plutôt que des évènements répétés de duplication et de divergence (Maisey 2009).

Chez de nombreux téléostéens, une nageoire adipeuse est présente, située entre les nageoires dorsale et caudale. Celle-ci constitue une nouveauté évolutive et pourrait représenter un autre module de nageoire distinct (Stewart and Hale 2013). Une nageoire adipeuse serait apparue indépendamment à au moins deux reprises, une première fois au sein des otophysiens, puis de nouveau chez les eutéléostéens (Stewart and Hale 2013). La nageoire adipeuse possède une anatomie plus rudimentaire comparativement aux autres nageoires, mais ceci ne semble pas résulter d'une évolution régressive à partir de nageoires précédemment plus élaborées (Sandon 1956). Il a été démontré récemment que la nageoire adipeuse chez le poisson chat de Günther (*Horobagrus brachysoma*) est sous contrôle musculaire : cette musculature résulte possiblement d'une co-option de modules développementaux associés à une partie de la musculature des autres nageoires (Stewart and Hale 2013).

Hypothèses de modularité des nageoires paires

Des hypothèses de modularité ont aussi été proposées pour les nageoires paires (Figure 4). Une première hypothèse quant à l'origine des nageoires paires est que les mécanismes moléculaires responsables de la formation des nageoires médianes ont été redéployés latéralement (Crotwell et al. 2001; Freitas et al. 2006; Crotwell and Mabee 2007; Hadzhiev et al. 2007; Freitas et al. 2014). Cette hypothèse est également appuyée par de nombreuses similitudes anatomiques et développementales entre les nageoires paires et médianes. Les nageoires dorsale, anale, pectorales et pelviennes sont structurellement similaires et sont composées d'une portion proximale avec des

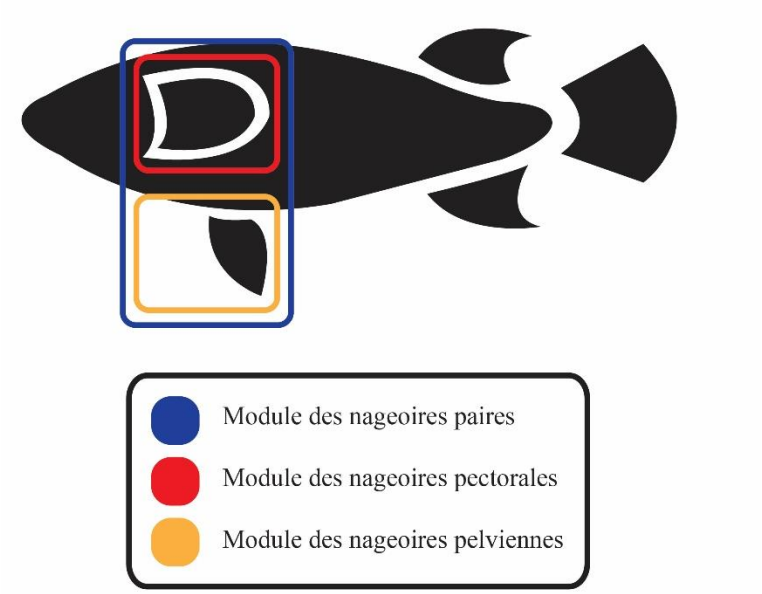

Figure 4 : Hypothèses de modularité suggérées pour les nageoires paires.

éléments de support endosquelettiques et une musculature associée, et d'une portion distale non-muscularisée, supportée par des rayons d'origine dermique (Bemis and Grande 1999; Lauder and Drucker 2004). Au cours du développement embryonnaire, les nageoires paires et médianes se développent et se différentient à partir de replis d'épithélium, les replis apicaux (*apical folds*) dans le cas des nageoires paires et le repli natatoire médian (*median larval finfold*) dans le cas des nageoires impaires (Ballard et al. 1993; van Eeden et al. 1996; Grandel and Schulte-Merker 1998; Bemis and Grande 1999; Abe et al. 2007). Contrairement au repli natatoire médian qui représente une structure continue à partir de laquelle les nageoires médianes se différencient, les replis apicaux des nageoires paires sont cependant interrompus dans la région située entre les nageoires pectorales et pelviennes en développement (Bemis and Grande 1999; Tanaka et al. 2002). Finalement il a été démontré que les nageoires paires et médianes partagent des similitudes importantes quant aux voies de signalisation moléculaires régissant leur développement (Freitas et al. 2006; Abe et al. 2007; Freitas et al. 2014).

Une autre hypothèse de modularité concernant les nageoires paires est que les nageoires pelviennes résulteraient d'une duplication de modules initialement associés aux nageoires pectorales. Les données paléontologiques (Coates 1993; Forey and Janvier 1993; Coates 1994; Shubin et al. 1997; Coates and Cohn 1998, 1999) et développementales (Ballard et al. 1993; Didier et al. 1998; Grandel and Schulte-Merker 1998; Faustino and Power 1999; Ruvinsky and Gibson-Brown 2000; Joss and Longhurst 2001) suggèrent qu'il est vraisemblable de considérer que les nageoires pectorales sont apparues avant les nageoires pelviennes au cours de l'histoire évolutive des poissons. Les nageoires pelviennes pourraient donc représenter une réitération de modules développementaux précédemment associés aux nageoires pectorales. Un scénario de duplication suivi de la dissociation du module des nageoires paires aiderait à expliquer comment les nageoires pectorales et pelviennes peuvent être modifiées ou perdues indépendamment l'une de l'autre au cours de l'évolution (Coates and Cohn 1998; Coates et al. 2002; Hall 2010).

L'hypothèse proposant que les nageoires pelviennes résultent d'un phénomène de duplication modulaire implique que les nageoires paires constituent des homologues sériés. En effet, les homologues sériés surviennent lorsque le programme développemental sous-jacent à une structure est dupliqué et ré-exprimé à un autre endroit dans l'organisme (Hall 1995; Young and Hallgrímsson 2005). Certains auteurs considèrent que les nageoires paires des gnathostomes sont effectivement des homologues sériés, notamment parce qu'elles partagent de nombreuses similitudes anatomiques et développementales (Shubin et al. 1997; Ruvinsky and Gibson-Brown 2000; Capdevila and Izpesúa Belmonte 2001; Shubin 2002). À l'inverse, d'autres auteurs argumentent que les nageoires paires des gnathostomes ne sont pas des homologues sériés puisque les nageoires pelviennes sont plus petites que les nageoires pectorales, que leur anatomie est plus rudimentaire, et que le patron phylogénétique des nageoires paires montre peu d'évidences pour une évolution concertée (Coates and

Cohn 1998, 1999; Coates et al. 2002). Pourtant, les membres pairs des tétrapodes constituent un exemple classique d'homologues sériés (Shubin et al. 1997; Ruvinsky and Gibson-Brown 2000; Hallgrímsson et al. 2002; Young and Hallgrímsson 2005; Young et al. 2010), et il est généralement admis que ceux-ci sont eux-mêmes homologues aux nageoires paires des poissons (Ahlberg 1989; Janvier 1996b; Shubin et al. 1997; Coates and Cohn 1998; Coates et al. 2002; Daeschler et al. 2006; Shubin et al. 2006; Shubin et al. 2009; Yano and Tamura 2013).

La problématique

La problématique de cette thèse s'inscrit dans un cadre fortement intégrateur qui unit la disparité morphologique observée entre les organismes à une propriété organisationnelle du vivant, la modularité, le tout dans le contexte des relations phylogénétiques au sein des vertébrés basaux. Que ce soit au cours de l'ontogénie ou de l'évolution, les modules sont considérés comme étant des unités quasi-indépendantes, ce qui leur permet de suivre des trajectoires développementales ou évolutives distinctes des autres modules (Simon 1962; Magwene 2001; Müller 2007). De ce fait, la modularité est considérée comme étant un aspect fondamental de l'évolvabilité (c'est-à-dire la capacité à évoluer) des systèmes biologiques (Bonner 1988; Raff 1996; Wagner 1996; Wagner and Altenberg 1996; Hendrikse et al. 2007). L'évolvabilité étant une propriété variationnelle ayant une incidence à l'échelle macroévolutive, une organisation plus ou moins modulaire permettrait d'expliquer comment la disparité morphologique peut s'accumuler différemment d'une lignée évolutive à l'autre (West-Eberhard 2003; Sanger et al. 2012).

L'objectif principal de ce projet doctoral est donc d'explorer la relation entre la disparité morphologique et la modularité, et ce en utilisant les poissons comme organismes modèles. Un aspect important de la disparité morphologique chez les poissons concerne l'organisation des nageoires. En effet, des changements dans la

configuration des nageoires sont fréquemment associés à des modifications dans l'écologie des espèces (Webb 1982; Lauder and Liem 1983; Webb 1984; Lauder and Drucker 2004; Shubin and Davis 2004). La modularité offre un cadre conceptuel avantageux pour étudier à la fois l'émergence de disparité morphologique dans la configuration des nageoires, mais également la séquence évolutive d'apparition de ces nageoires. Certaines nageoires pourraient être apparues en tant que nouveautés évolutives suite à des processus de duplication de modules de nageoires préexistants, poue ensuite se découpler ou diverger au cours de l'évolution.

Un certain nombre de modules ont déjà été suggérés en ce qui concerne les nageoires paires et médianes chez les poissons. Ces hypothétiques modules de nageoires sont largement appuyés par des données développementales, mais pour la plupart n'ont pas fait l'objet de démonstrations statistiques rigoureuses. De plus, les définitions de certains de ces modules proposés pour les nageoires ne correspondent pas aux types de modules qui sont habituellement discutés selon les théories de la biologie du développement ou de la biologie évolutive. Les modules de patrons de formation proposés par Mabee et al. (2002) sont basés sur l'observation de covariation dans les séquences de formation des éléments squelettiques de support des nageoires. Ceci soulève une ambiguïté puisqu'ils pourraient alors aussi bien être considérés comme des modules développementaux ou des modules variationnels. Quant aux modules de positionnement des nageoires dorsale et anale, ceux-ci sont inférés en fonction d'observations faites sur de nombreuses espèces, et résultent donc de comparaisons à une échelle macroévolutive. Pour cette raison, ces modules de positionnement pourraient être considérés comme d'hypothétiques modules évolutifs. Cependant, la covariation dans le positionnement des nageoires pourrait aussi être analysée à une échelle microévolutive, ce qui permettrait d'identifier des modules variationnels. Un aspect fondamental de cette étude est donc de vérifier si les modules identifiés en fonction de séquences développementales, suggérant donc l'implication de modules développementaux, correspondent bien aux modules variationnels à l'échelle

microévolutive, et si ceux-ci correspondent à leur tour aux modules évolutifs à l'échelle macroévolutive.

Les questions principales qui sont adressées dans le cadre de cette thèse sont les suivantes. (1) La disparité morphologique en termes de combinaisons de nageoires est-elle répartie uniformément au sein de la phylogénie des poissons, ou bien certaines lignées évolutives sont-elles plus disparates ? (2) Les connaissances quant à la séquence évolutive d'apparition des nageoires peuvent-elles être affinées ? (3) Des modules variationnels des nageoires peuvent-ils être identifiés à une échelle microévolutive ? (4) Des modules évolutifs de nageoires peuvent-ils être identifiés à une échelle macroévolutive, soit parce que certaines nageoires covarient dans leur présence/absence ou dans leur positionnement ? (5) Les patrons d'intégration morphologique aux échelles micro- et macroévolutives correspondent-ils ? (6) Et finalement, existe-t-il une relation entre les patrons d'intégration morphologique observés, la disparité et les taux d'évolution morphologique ?

Objectifs de recherche et méthodologie utilisée

Cette thèse doctorale comportait trois objectifs principaux. Le premier objectif était de décrire et d'analyser les patrons de disparité morphologique en termes de présence/absence et du nombre des nageoires médianes et paires au sein des différents ordres de poissons, aussi bien actuels que fossiles, et ce dans une perspective phylogénétique. Le second objectif était de caractériser la variation morphologique en termes de positionnement des nageoires médianes et paires à l'échelle microévolutive, dans le but d'identifier des modules variationnels. Quant au troisième objectif, celui-ci est similaire au second mais cette fois à l'échelle macroévolutive, dans le but d'identifier des modules évolutifs régissant le positionnement des nageoires paires et médianes. Une description plus exhaustive de ces objectifs ainsi qu'une synthèse des méthodes qui ont été utilisés pour les compléter seront maintenant présentés.

1er objectif : Décrire et analyser les patrons de disparité morphologique en termes de présence/absence et du nombre des nageoires médianes et paires au sein des différents ordres de poissons, aussi bien actuels que fossiles, selon une perspective phylogénétique.

Le premier objectif était de caractériser les patrons de disparité morphologique en termes de configuration des nageoires dans un contexte phylogénétique et d'analyser la covariation dans la présence/absence et le nombre de chacune des nageoires médianes et paires. Plus spécifiquement, cet objectif incluait de vérifier si certaines lignées évolutives de poissons sont plus disparates dans leurs configurations de nageoires, d'explorer des scénarios évolutifs d'apparition séquentielle des nageoires, et d'inférer la présence de modules évolutifs à partir des données de présence/absence et de nombre de nageoires. À ces fins, une matrice a été assemblée contenant les données de présence/absence et de nombre de chacune des nageoires médianes et paires pour un total de 2730 espèces, parmi lesquelles 607 taxons fossiles et 2123 taxons actuels. L'incorporation de données sur le registre fossile était nécessaire puisque cela permet de mettre en évidence les conditions plésiomorphes au niveau du groupe, notamment pour les agnathes où les seuls représentants actuels sont les myxines et les lamproies.

La complétion du premier objectif a aussi nécessité la production d'un super-arbre des poissons à l'échelle de l'ordre sur lequel les données de présence/absence et de nombre de nageoires médianes et paires ont été superposées. En effet, une phylogénie des ordres de poissons incorporant la totalité de l'étendue phylogénétique de cette étude, soit des céphalochordés aux premiers tétrapodes, n'était pas disponible dans la littérature. Les super-arbres constituent une méthode adéquate pour synthétiser les résultats d'un grand nombre d'hypothèses phylogénétiques existantes, particulièrement lorsqu'une approche par évidence totale (*Total Evidence approach*) n'est pas

disponible (Bininda-Emonds and Sanderson 2001; Bininda-Emonds et al. 2002; Baum and Ragan 2004).

La superposition des données de présence/absence et de nombre des nageoires sur le super-arbre a permis d'identifier les régions au sein de la phylogénie des poissons qui sont caractérisées par une disparité plus importante en termes de patrons de configurations des nageoires. La superposition de ces données a aussi été utilisée afin d'explorer des scénarios évolutifs d'émergence séquentielle des nageoires médianes et paires au cours de l'histoire évolutive des poissons, et d'apprécier qualitativement s'il y a de la congruence dans l'addition ou dans la perte de certaines nageoires. Une combinaison d'analyses exploratoires et de tests d'hypothèses ont également été utilisés afin d'analyser les patrons de cooccurence des nageoires médianes et paires. Dans un contexte où certaines paires de nageoires formeraient des modules évolutifs, on pourrait s'attendre à ce que la coordination dans la perte ou dans la duplication de ces nageoires soient plus fréquentes que la perte de l'une sans la perte de l'autre.

2^{ième} objectif : Caractériser la variation morphologique en termes de positionnement des nageoires médianes et paires à l'échelle microévolutive, dans le but d'identifier des modules variationnels.

Le deuxième objectif était de vérifier si, à l'échelle de l'espèce, les patrons de covariation dans le positionnement des nageoires médianes et paires correspondent bien aux hypothèses de modularité suggérées entre autres par les données développementales. Pour ce deuxième objectif qui visait à déterminer si certaines combinaisons de nageoires formaient des modules variationnels, nous avons utilisé des échantillons provenant de deux espèces de Cyprinidae, soit le poisson-zèbre (*Danio rerio*) et le ventre rouge du Nord (*Chrosomus eos*).

Une approche basée sur l'utilisation de la morphométrie géométrique a été préconisée. Plutôt que d'utiliser des mesures linéaires ou volumétriques, la morphométrie géométrique utilise les coordonnées cartésiennes de points de repères fixes appelés "landmarks" qui sont positionnés à des endroits spécifiques sur les structures morphologiques étudiées (Bookstein 1991; Zelditch et al. 2012). Un avantage important dans l'utilisation de morphométrie géométrique est que l'emphase est mise sur la géométrie de la structure dans sa totalité, et donc une quantité beaucoup plus importante d'information sur la forme est retenue comparativement à des combinaisons de mesures linéaires (Zelditch et al. 2012). La majorité des analyses qui visent à quantifier l'intégration morphologique, et par extension à tester des hypothèses de modularité, considèrent que des landmarks seront intégrés les uns aux autres s'ils sont corrélés dans leur variation (Klingenberg 2008).

Afin d'analyser et de comparer les patrons d'intégration morphologique et de modularité chez *D. rerio* et *C. eos*, une série de 19 hypothèses *a priori* de modularité ont d'abord été formulées. Ces hypothèses de modularité ont été élaborées en fonction de modules de nageoires précédemment suggérés dans la littérature (p. ex. Mabee et al. 2002; Shubin and Davis 2004; Hall 2010; Grünbaum et al. 2012), et en fonction de données développementales et paléontologiques, et de relations fonctionnelles et topologiques entre les structures. Quatre méthodes ont été utilisées afin de tester la qualité d'ajustement des hypothèses de modularité aux données observées : le coefficient RV (Klingenberg 2008, 2009), la corrélation entre des matrices de corrélation attendues et observées (Monteiro et al. 2005), la modélisation graphique (Magwene 2001, 2009) et la méthode du minimum de déviance (Márquez 2008).

3^{ième} objectif : Caractériser la variation morphologique en termes de positionnement des nageoires médianes et paires à l'échelle macroévolutive, dans le but d'identifier des modules évolutifs.

Le troisième objectif était de vérifier si, à l'échelle macroévolutive, les patrons de covariation dans le positionnement des nageoires médianes et paires permettaient d'identifier des modules évolutifs. Plus spécifiquement, la modularité est associée à certaines conséquences macroévolutives et pourrait notamment avoir une incidence sur les processus de disparification (West-Eberhard 2003). Ce troisième objectif incorporait donc de vérifier si une relation existe entre la modularité évolutive et l'ampleur de la disparité morphologique observée chez les poissons, possiblement par l'entremise de changements dans les taux d'évolution morphologique. Un autre aspect important du troisième objectif était de vérifier si il y une correspondance entre les patrons d'intégration morphologique et de modularité entre les échelles micro- et macroévolutives.

Afin de compléter le troisième objectif, une base de données de photographies de spécimens en vue latérale a été assemblée, incorporant 58 espèces d'actinoptérygiens. Pour permettre la comparaison avec les résultats du second chapitre de cette thèse doctorale, seules les espèces possédant la même configuration de nageoires que les deux espèces de Cyprinidae utilisés pour les analyses de modularité variationnelle ont été considérées. Les espèces possédant des nageoires coalescentes (par exemple avec une fusion des nageoires dorsale, anale et caudale), celles possédant plus d'une nageoire dorsale ou anale, et celles où l'une ou l'autre des nageoires médianes ou paires étaient absentes n'ont donc pas été prises en compte. Ceci était nécessaire afin de permettre l'utilisation de la même série de 14 landmarks homologues. Toujours à des fins de comparaison entre les analyses aux échelles micro- et macroévolutives, les même 19 hypothèses de modularité mentionnées précédemment ont été testées. Cinq hypothèses supplémentaires ont cependant été ajoutées basées sur des tendances évolutives dans les patrons de configuration des nageoires chez les actinoptérygiens. Ainsi au total, 24 hypothèses de modularité ont été analysées. Trois méthodes ont été utilisées pour tester les hypothèses de modularité évolutive : la modélisation graphique

(Magwene 2001, 2009), la méthode du minimum de déviance (Márquez 2008), et la mesure du ratio de covariance (CR) (Adams 2016).

Dans des analyses de modularité évolutive, il est important de prendre en compte le contexte phylogénétique dans les analyses (Zelditch et al. 2012; Klingenberg 2013). En effet, il est attendu que des groupes apparentés phylogénétiquement seront plus similaires simplement parce qu'ils partagent davantage d'histoire évolutive (Felsenstein 1985; Harvey and Pagel 1991). Afin de prendre en considération le signal phylogénétique, nous avons utilisé une phylogénie des actinoptérygiens récemment publiée (Near et al. 2012) qui présentait une étendue phylogénétique comparable à notre échantillonnage de taxons. De plus, la méthode du ratio des taux évolutifs a été utilisée (Denton and Adams 2015) afin de vérifier si des différences significatives existaient dans les taux d'évolution entre les modules évolutifs définis par chacune des hypothèses de modularité *a priori*. Cette méthode permet l'estimation et la comparaison de taux d'évolution morphologique entre diverses partitions en prenant en considération le contexte phylogénétique (Denton and Adams 2015).

CHAPITRE I

MODULES DE NAGEOIRES : UNE PERSPECTIVE ÉVOLUTIVE SUR LA DISPARITÉ DES APPENDICES CHEZ LES VERTÉBRÉS BASAUX

1.1 Résumé

Les poissons sont un groupe extrêmement diversifié qui présente en plus une importante disparité morphologique concernant de nombreux aspects de leur anatomie, incluant notamment des différences dans la configuration des nageoires. Plus spécifiquement, les poissons diffèrent quant au nombre de nageoires présentes, ainsi que dans la structure, la forme et la taille de celles-ci. Il est difficile d'expliquer comment les poissons ont acquis cette remarquable disparité morphologique considérant l'inexistence d'une synthèse exhaustive de l'histoire évolutive des appendices locomoteurs au sein de ce groupe. La modularité des nageoires pourrait fournir une explication non seulement pour la disparité observée en termes de configurations de nageoires, mais aussi pour l'apparition séquentielle de nouvelles nageoires. La modularité est considérée comme un prérequis important pour l'évolvabilité des systèmes biologiques, en permettant à certains modules d'être optimisés sans interférer avec d'autres. Des similarités développementales entre certaines nageoires suggèrent déjà qu'elles forment des modules développementaux au cours de l'ontogénie. À l'échelle macroévolutive, ces modules développementaux pourraient agir comme des unités sur lesquelles la sélection peut agir, et ainsi contribuer à la disparité dans l'organisation des nageoires. Cette étude analyse la disparité dans les configurations de nageoires selon une perspective phylogénétique, en focalisant sur la présence/absence et le nombre de chacune des nageoires médianes et paires. Les patrons de disparité morphologique ont été explorés en superposant les caractères de présence/absence des nageoires sur un super-arbre phylogénétique des ordres de poissons. Parmi les agnathes, la disparité dans la configuration des nageoires résulte de

l'apparition séquentielle de nouvelles nageoires donnant lieu à des combinaisons variées de celles-ci. Les nageoires médianes et paires seraient toutes deux apparues d'abord sous la forme de structures allongées avant d'être remplacées par des nageoires aux bases d'insertion plus exigües. Chez les chondrichthyens, la disparité dans la configuration des nageoires relève surtout de la perte de nageoires médianes. Chez les actinoptérygiens, la disparité dans la configuration des nageoires implique à la fois la perte de nageoires, l'addition de nouvelles nageoires (p. ex. nageoire adipeuse) et la duplication coordonnée des nageoires dorsale et anale. Certaines paires de nageoires, notamment les nageoires dorsale/anale et pectorales/pelviennes, ne sont pas indépendantes dans la distribution de leurs états de caractères, ce qui supporte des hypothèses basées sur des observations morphologiques et développementales que ces paires de nageoires forment des modules évolutifs. Ces résultats suggèrent que les nageoires dorsale/anale et pectorales/pelviennes forment deux modules évolutifs distincts. De plus, le module dorsal/anal pourrait être niché dans un module plus inclusif des nageoires médianes. Parce que les hypothèses de modularité qui ont été analysées sont également supportées par des données développementales et variationnelles, cela constitue un exemple marquant qui relie des modules développementaux, variationnels et évolutifs.

Cet article, intitulé *Fin modules: An evolutionary perspective on appendage disparity in basal vertebrates*, a été corédigé par moi-même ainsi que par Miriam L. Zelditch et Richard Cloutier et a été publié dans le journal international *BMC Biology* en avril 2017. Le cadre conceptuel de ce premier chapitre de ma thèse a été élaboré par Richard Cloutier et par moi-même. Les aspects méthodologiques du chapitre ont été développés par Richard Cloutier et par moi-même, avec l'aide du Dr. Alain Caron dans le choix des analyses statistiques. En tant que premier auteur, mes contributions incluent notamment la revue de la littérature pertinente, la préparation des bases de données, la complétion des analyses phylogénétiques et statistiques, et la production des figures et du matériel supplémentaire. J'ai rédigé la première version du manuscrit, et tous les

auteurs ont contribué aux versions subséquentes jusqu'à la production de la version finale. Une partie des résultats ont été présentés sous la forme d'affiches scientifiques dans deux congrès internationaux, soit lors du *12th International Symposium on Early Vertebrates/Lower Vertebrates* en juin 2011 à Dallas (Texas), et lors du *1st Joint Congress on Evolutionary Biology* en juillet 2012 à Ottawa (Ontario). Ces résultats ont aussi été présentés sur invitation du Dr. Brian K. Hall dans le cadre d'un *Mini-Symposium on Fish Evo-Devo* qui s'est déroulé au Mount St-Vincent University, à Halifax (Nouvelle-Écosse), en février 2015. Une revue exhaustive de la littérature a été nécessaire en ce qui concerne l'évolution des nageoires médianes et paires et leurs relations d'homologies entre les groupes de poissons, cela afin de justifier le codage des caractères utilisés. Cette revue de la littérature constitue la majeure partie d'un article en préparation pour soumission dans le journal international *Historical Biology*.

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Fin modules: An evolutionary perspective on appendage disparity in basal vertebrates

1.2 Abstract

Fishes are extremely speciose and also highly disparate in their fin configurations, more specifically in the number of fins present as well as their structure, shape and size. How they achieved this remarkable disparity is difficult to explain in the absence of any comprehensive overview of the evolutionary history of fish appendages. Fin modularity could provide an explanation for both the observed disparity in fin configurations and the sequential appearance of new fins. Modularity is considered as an important prerequisite for the evolvability of living systems, enabling individual modules to be optimized without interfering with others. Similarities in developmental patterns between some of the fins already suggest that they form developmental modules during ontogeny. At a macroevolutionary scale, these developmental modules could act as evolutionary units of change and contribute to the disparity in fin configurations. This study addresses fin disparity in a phylogenetic perspective, while focusing on the presence/absence and number of each of the median and paired fins. Patterns of fin morphological disparity were assessed by mapping fin characters on a new phylogenetic supertree of fish orders. Among agnathans, disparity in fin configurations results from the sequential appearance of novel fins forming various combinations. Both median and paired fins would have appeared first as elongated ribbon-like structures, later replaced by more constricted appendages. Among chondrichthyans, disparity in fin configurations relates mostly to median fin losses. Among actinopterygians, fin disparity involves fin losses, the addition of novel fins (e.g., adipose fin), and coordinated duplications of the dorsal and anal fins. Furthermore, some pairs of fins, notably the dorsal/anal and pectoral/pelvic fins, show non-independence in their character distribution, supporting expectations based on developmental and morphological evidence that these fin pairs form evolutionary

modules. Our results suggest that the pectoral/pelvic fins, and the dorsal/anal fins form two distinct evolutionary modules, and that the latter is nested within a more inclusive median fins module. Because the modularity hypotheses that we are testing are also supported by developmental and variational data, this constitutes a striking example linking developmental, variational and evolutionary modules.

KEYWORDS: fishes, median fins, paired fins, morphological disparity, phylogenetic supertree, evolutionary modularity, agnathans, gnathostomes, chondrichthyans, osteichthyans.

1.3 Introduction

Fishes comprise the most basal representatives of the vertebrate lineage, a paraphyletic grouping that includes an astounding ~32 000 living species (Nelson et al. 2016). Fishes display a correspondingly high level of disparity in many aspects of their body plan (Figure 5). For centuries, it has been recognized that part of this disparity is due to the numerous fin configurations, including the number of fins, their size, their position on the body and their types of skeletal support (Lacépède 1798; Cuvier and Valenciennes 1828; Aristotle et al. 1878). Fins can be either median (dorsal, anal, caudal and adipose fins) or paired appendages (pectoral and pelvic fins) that are used primarily for the purpose of locomotion. Morphological disparity in fin configurations of living fishes can readily be observed when considering the presence or absence of these appendages: examples of fin losses are known for each of the median and paired fins, including the caudal fin (e.g., *Mola mola*). Alternatively, fins can also be duplicated, or even triplicated (e.g., dorsal fins in *Gadus morhua*). In some cases entirely new fins can emerge, as in the case of the adipose fin in some teleosts (Stewart et al. 2014).

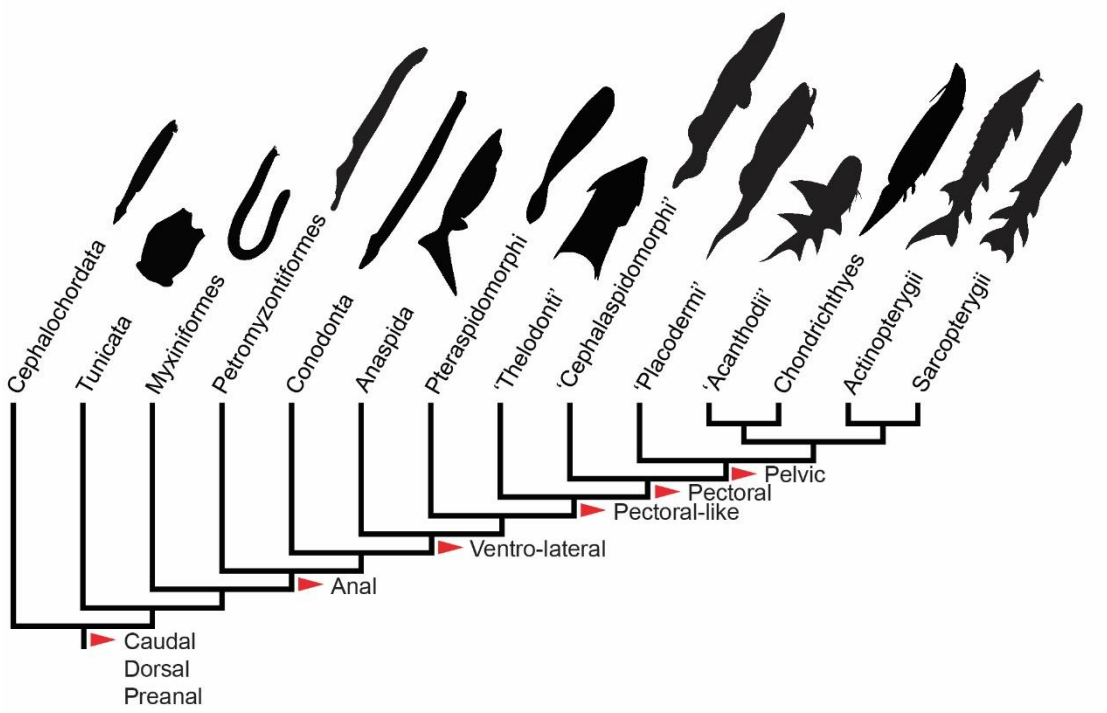

Figure 5: A sample of the disparity in fin configurations in extant and extinct fishes. The phylogenetic framework is a simplified version of the results of the supertree analysis (Figure 6). Nodes where new fins are sequentially added are identified.

The evolutionary sequence leading to the origin of fish appendages has not been completely resolved yet [although a good synthesis of what is known at the molecular level is provided in Freitas et al. (2014)]. It is generally acknowledged that fins first appeared as median dorsal and ventral structures during the Lower Cambrian (*ca* 535 Ma): the oldest known vertebrate fossils display well-developed median fins but no paired fins (Shu et al. 1999; Shu et al. 2003a; Zhang and Hou 2004). The anaspids, a group of jawless fishes, are the most primitive known vertebrates with unambiguous paired fins (Coates and Cohn 1998). However, the most basal vertebrates that conclusively display endoskeletal structures and associated musculature in paired appendages are among another group of jawless fishes, the osteostracans (Forey 1995; Coates and Cohn 1998; Coates 2003). The osteostracan paired fins are considered by

most as homologous to the pectoral fins of jawed vertebrates (e.g., Forey and Janvier 1993, 1994; Coates 2003; Sansom 2009), while the pelvic fins appeared later on among stem gnathostomes (Janvier 1996b; Shubin et al. 1997; Zhu et al. 2012b; Sansom et al. 2013). Thus, the fossil record indicates that the pectoral fins appeared before the pelvic fins (Coates 1993, 1994; Coates and Cohn 1998).

One potential explanation for both the emergence of new fins and the observed disparity in fin configurations is that fins are modular. Modularity, defined most broadly, means that organisms can be decomposed into smaller components which are termed modules (Wagner 1996; Winther 2001; Klingenberg 2008). Modules are therefore discrete and internally coherent units that may develop and also evolve quasi-independently from other modules (Simon 1962; Magwene 2001; Müller 2007). There are different kinds of modules that are defined according to the processes in which they are involved. Developmental modules are parts of an organism that are quasi-autonomous in their patterns of formation and differentiation (Raff 1996; Wagner and Mezey 2004; Wagner et al. 2007), variational modules comprise traits that covary within populations (Cheverud 1996a; Wagner and Altenberg 1996; Wagner et al. 2007) and evolutionary modules comprise traits that co-evolve (Cheverud 1982, 1996a; Brandon 1999). Because of their quasi-independence, developmental modules may correspond to variational or evolutionary modules as well (Brandon 1999; Müller 2007). Modules may also be susceptible to duplication, dissociation, divergence and/or co-option (Raff 1996). This can lead to the repetition of individual structures that, if decoupled, can subsequently follow their own evolutionary trajectories (Raff 1996; Winther 2001; Monteiro 2008). Such a process of modular duplication followed by decoupling has been hypothesized to facilitate the emergence of morphological and/or functional innovations (Riedl 1978; Weiss 1990; Raff 1996; Winther 2001; Savriama et al. 2016). Thus, the concept of modularity is well suited to investigate the functional and developmental disparity observed in organisms (Wagner et al. 2007), and it may account for the high disparity of fin configurations in fishes.

Hypotheses of modularity have already been proposed for both median and paired fins in fishes. Four fundamental modules involved in the positioning and patterning of median fins have been hypothesized for living actinopterygians (ray-finned fishes): the designated positioning modules refer to similar positions along the body axis between the dorsal and anal fins, while the designated patterning modules refer to similarities in anatomical development between these two fins (Mabee et al. 2002). Some of these patterning modules have also been identified in fossil actinopterygians and sarcopterygians (lobe-finned fishes), suggesting that they could have been inherited from a common ancestor to all osteichthyans (bony fishes, comprising all actinopterygians and sarcopterygians) (Cloutier 2010). Developmental evidence from the catshark (*Scyliorhinus canicula*) also indicates that modules might be involved in the positioning of the dorsal and anal fins in chondrichthyans (cartilaginous fishes) (Freitas et al. 2006). It has also been suggested that developmental mechanisms could have been co-opted from the median fins, leading to the emergence of the paired fins (Crotwell et al. 2001; Freitas et al. 2006; Crotwell and Mabee 2007; Hadzhiev et al. 2007; Freitas et al. 2014). Furthermore, most authors generally consider that the pectoral fins appeared before the pelvic fins (Coates 1993; Forey and Janvier 1993; Coates 1994; Shubin et al. 1997; Coates and Cohn 1998), leading to the hypothesis that the pelvic fins might represent a reiteration of the pectoral fins module. Duplication of a paired fins module followed by decoupling would help to explain why pectoral and pelvic fins can be altered or lost independently (Coates and Cohn 1998; Coates et al. 2002; Hall 2010).

Modularity can offer a valuable framework to investigate both the emergence of morphological disparity in fin configurations, and the sequential appearance of fins in vertebrates. New fins could arise through processes such as fin module duplications that could subsequently become decoupled on an evolutionary timescale. However, two main issues complicate the interpretation of these evolutionary transformations of

fins: (1) the lack of consensus regarding the homology of structures found in early vertebrate appendages (Johanson 2010; see Annexe B) and (2) the lack of consensus concerning phylogenetic relationships among fishes (e.g., Forey 1995; Janvier 1996a; Donoghue et al. 2000; Donoghue and Smith 2001; Brazeau 2009; Sansom et al. 2010; Turner et al. 2010; Davis et al. 2012; Zhu et al. 2013; Dupret et al. 2014; Giles et al. 2015c; Long et al. 2015; Burrow et al. 2016; Keating and Donoghue 2016; Qiao et al. 2016). With this in mind, this study has two principal objectives. The first is to characterize the morphological disparity in fin configurations in an evolutionary perspective, and to investigate possible scenarios for the sequential appearance of each one of the median and paired fins. This evolutionary perspective required a phylogenetic context for the analyses. Because a complete phylogeny of extinct and extant fishes at the ordinal level has not yet been published, we used a supertree approach to summarize findings from recent investigations of basal vertebrate interrelationships. The second objective is to analyze covariation patterns between fins in terms of their presence/absence at a macroevolutionary scale, which could indicate their evolutionary modularity. We predicted that fins that are hypothesized to share developmental or evolutionary modules controlling their positioning and/or patterning should also covary in their presence/absence data.

1.4 Methods

1.4.1 Fin presence/absence dataset

1.4.1.1 *Taxonomic selection*

A dataset was constructed using a sample of representative species from 144 orders of fishes. Ordinal classification of extant species followed Nelson et al. (2016) and Fishbase (Froese and Pauly 2016). For fossil taxa, ordinal classifications of different authors have been used in relation to the taxonomic group, with some minor taxonomic

modification based on most recent literature: Janvier (1996b) for agnathans in general; Märss et al. (2007) for thelodonts; Denison (1978) and Young (2010) for placoderms; Nelson et al. (2016) for acanthodians; Ginter et al. (2010) for elasmobranchs and Stahl (1999) for holocephalians; Nelson et al. (2016) for actinopterygians; and Cloutier & Ahlberg (1996) for sarcopterygians. The sample comprised a total of 2730 taxa (607 extinct, 2123 extant), representing about 9% of current estimates of fish species richness [~32 000 living species (Nelson et al. 2016)]. Species were selected to maximize diversity within each one of the orders. This was done by sampling individual orders proportionately to their species richness while maximizing the number of families and genera taken into account. Special care was taken not to oversample extreme morphologies. For the fossil data, a selection was made based on the availability and completeness of morphological data. Furthermore, scoring of fin characters of fossil taxa was based on photographs and on the descriptive work, and not on published paleontological reconstructions. The inclusion of fossil taxa is important to reveal basal character states which might not be observable in more recent and derived forms.

1.4.1.2 *Appendage terminology*

The extensive disparity in fin morphologies and the debated homologies of some of the fins among different groups of fishes required that we came up with consistent defining criteria for each of them. We did not define the fins based on strict-homology criteria in order to be able to score for the totality of the disparity encountered in the analysis. Patterson (1982) proposed that three criteria should be used to define homologous structures: (1) similarity (topographical correspondence and ontogenetic transformation), (2) conjunction (or anatomical singularity) and (3) congruence (phylogenetic congruence with other homologies). In our case, the identity of the fins was established largely on the basis of a positional criterion, which is one of these criteria (topographical similarity) used to assess homology between structures

Table 2: Terminology used to define fins for the scoring of characters among taxa.

Terms used in this paper	Definition	Other terms that have been used
Median ventral fin	An unpaired ventral finfold that can be inserted either anteriorly (e.g., some Myxiniformes) or posteriorly to the anus, and anteriorly to the anal fin when it is present [e.g., some Stomiidae, Paralepididae and Phallostethidae (Teleostei)]	Preanal finfold (or skinfold); ventral adipose fin
Ventrolateral paired fins	Ventrolaterally positioned fins or fin supports placed along the trunk that are generally long-based and cannot be homologized to pectoral or pelvic fins.	Ventrolateral finfolds; intermediate spines; prepelvic spines
Pectoral fins	Narrow-based paired fins inserted on the thorax close to the gill openings.	Suprabranchial fins; paired flaps; pectoral flaps; pectoral swimming appendages
Pelvic fins	Ventrally inserted narrow based paired fins, always located anteriorly to the anus/cloaca.	Ventral fins
Dorsal fin(s)	Fins located on the dorsal midline of the body, between the head and the tail.	
Anal fin(s)	Fins located on the ventral midline between the anus (or cloaca) and the tail.	
Adipose fin	A small non-rayed fin usually located medially between the dorsal and caudal fins; this median fin is present among several groups of basal euteleosts.	Fatty fin; dorsal organ; dorsal filament
Caudal fin	The caudal fin is located at the extremity of the tail.	Tail fin

(Patterson 1982). Structural and ontogenetic criteria were also used when position alone was insufficient to clearly define some fins and when these data were available from the literature. The definitions used for the scoring of fin characters are provided in Table 2.

1.4.1.3 *Appendage coding*

Species considered in the analyses were scored for the presence or absence and the number of each one of the fins: median ventral fin (0 or 1), ventrolateral paired fins (0 or 1), pectoral fins (0 or 1), pelvic fins (0 or 1), dorsal fin (0, 1, 2 or 3), anal fin (0, 1 or 2), adipose fin (0 or 1) and caudal fin (0 or 1). The scoring reflected the number of each fin present and had no implications as to the plesiomorphic or apomorphic condition of characters. Presence or absence of each of the fins was assessed based on multiple sources including specimen descriptions, photographic material, radiographs, illustrations and paleontological reconstructions.

1.4.2 Fish supertree

Our investigation of fin morphological disparity required a phylogenetic framework. Yet, phylogenies of basal vertebrates have not reached a generalized consensus (e.g., Forey 1995; Janvier 1996a; Donoghue et al. 2000; Donoghue and Smith 2001; Brazeau 2009; Sansom et al. 2010; Turner et al. 2010; Davis et al. 2012; Zhu et al. 2013; Dupret et al. 2014; Giles et al. 2015c; Long et al. 2015; Burrow et al. 2016; Keating and Donoghue 2016; Qiao et al. 2016) and a complete phylogeny of fossil and extant fishes at the ordinal level that encompasses the entire taxonomical span considered in this study is not currently available.

The phylogenetic framework was constructed using a supertree approach, more specifically with the Matrix Representation with Parsimony (MRP) algorithm (Baum

1992; Ragan 1992; Baum and Ragan 2004), which is the most commonly used method (Bininda-Emonds and Sanderson 2001; Bininda-Emonds et al. 2002; Bininda-Emonds 2004; Gatesy and Springer 2004). The MRP method is well-suited for inferring topologies from diverse partially overlapping datasets (Baum 1992; Ragan 1992; Purvis 1995b; Bininda-Emonds and Bryant 1998; Baum and Ragan 2004), notably for the joint analysis of fossil and extant data (Bininda-Emonds et al. 2002; Klug and Kriwet 2010). A set of 118 source trees (see Annexe C) was compiled. Selected source trees had to have been generated using modern computer-based phylogenetic analyses (the analyses used were published between 1986 and September 2016), and resulted from either morphological or molecular datasets. The supertree was constructed using the phangorn package (Schliep 2011) in R version 3.2.4 (R Core Team 2016). Source trees were simplified at the ordinal level whenever necessary. Some fish orders continue to be used for taxonomic simplification even though they are most likely paraphyletic or polyphyletic (e.g., "Climatiiformes", "Perciformes", "Osteolepiformes"). These orders were subdivided into smaller units that could be assigned to multiple nodes in individual source trees prior to generating the consensus topology. Phylogenetic supertrees were reconstructed with the maximum parsimony function that generates a single most parsimonious solution, and with Nixon (1999)'s parsimony ratchet that performs heuristic searches and generates a set of most parsimonious trees (Schliep 2011).

In order to manage the broad phylogenetic scope of the source trees, five separate supertree analyses were conducted [i.e., "agnathans", basal gnathostomes (placoderms and acanthodians), chondrichthyans, actinopterygians and sarcopterygians]. The interrelationships among these larger more inclusive groups are well resolved, and the resulting trees from each individual analysis were thus combined to generate the complete supertree of fishes. An exception to this concerns the interrelationships between placoderms, acanthodians and crown gnathostomes, which are currently strongly debated. For this purpose, the supertree analysis focusing on these stem

gnathostome groups incorporated chondrichthyans and osteichthyans as terminal branches.

The MRP supertree method combines source trees with the assumption that datasets are independent (Bininda-Emonds and Sanderson 2001; Bininda-Emonds et al. 2004; Bryant 2004; Gatesy and Springer 2004). However, in this case some source trees cannot be considered as independent, particularly for the fossil groups where phylogenetic analyses often build upon previously published data matrices, adding or re-scoring taxa and characters. To reduce this bias, care was taken to select source trees where either the character sets or the list of taxa had been substantially modified. The impracticability of this assumption of total independence of source trees is a well-known issue in supertree constructions, and non-independence is unlikely to be completely eliminated (Purvis 1995a; Bininda-Emonds et al. 1999; Springer and de Jong 2001; Bininda-Emonds et al. 2002; Gatesy et al. 2002; Bininda-Emonds et al. 2004; Gatesy and Springer 2004).

Phylogenetic supertrees have also been criticized for losing contact with the primary data from which they are derived (Rodrigo 1993, 1996; Novacek 2001; Springer and de Jong 2001; Gatesy et al. 2002; Bryant 2004). Bryant (2004, p. 366) added that MRP supertrees are likely to violate at least some phylogenetic principles and are consequently best considered as a « *heuristic synthesis of available hierarchical information, rather than the products of rigorous phylogenetic analysis*. » Nonetheless, phylogenetic supertrees provide a reasonable alternative to an analysis based on total evidence in situations where such an approach is unavailable (Bininda-Emonds and Sanderson 2001; Bininda-Emonds et al. 2002; Baum and Ragan 2004).

1.4.3 Mapping of the fin characters on the supertree

A summary of the presence/absence data was mapped on the supertree (Figure 6). This was done by compiling the observed character states for individual fins within each of the orders (see Annexe D), and mapping the information on the terminal branches of the tree. This allowed us to explore possible scenarios of sequential appearance of fins, as well as to determine where most of the morphological disparity in fin configurations was concentrated in the phylogeny of fishes.

1.4.4 Covariation in the number of fins present

Multiple correspondence analyses were used as an exploratory method to investigate covariation among fins in the presence/absence data. Relationships between pairs of fins were also statistically tested using Fisher's exact test. Since Fisher's exact test only tells us if there is non-independence in frequencies of observations between two qualitative variables, we used Spearman's rank correlation coefficients to establish the direction of the relationships between variables. For each pair of fins, a positive correlation indicates that they tend to be jointly present, or jointly absent. Alternatively, a negative correlation means that the variables have opposite trends: for instance one fin is present while the other is absent.

As described in the previous section, prior to running the analyses, the dataset was summarized by identifying all of the unique fin combinations within individual orders. An analysis was also performed by identifying all unique combinations for the entire dataset, excluding combinations that contained missing data, resulting in 51 fin combinations. Sensitivity analyses were performed to assess the effect of missing data: this was done by running separate analyses where taxa with the most missing fin characters were sequentially removed.

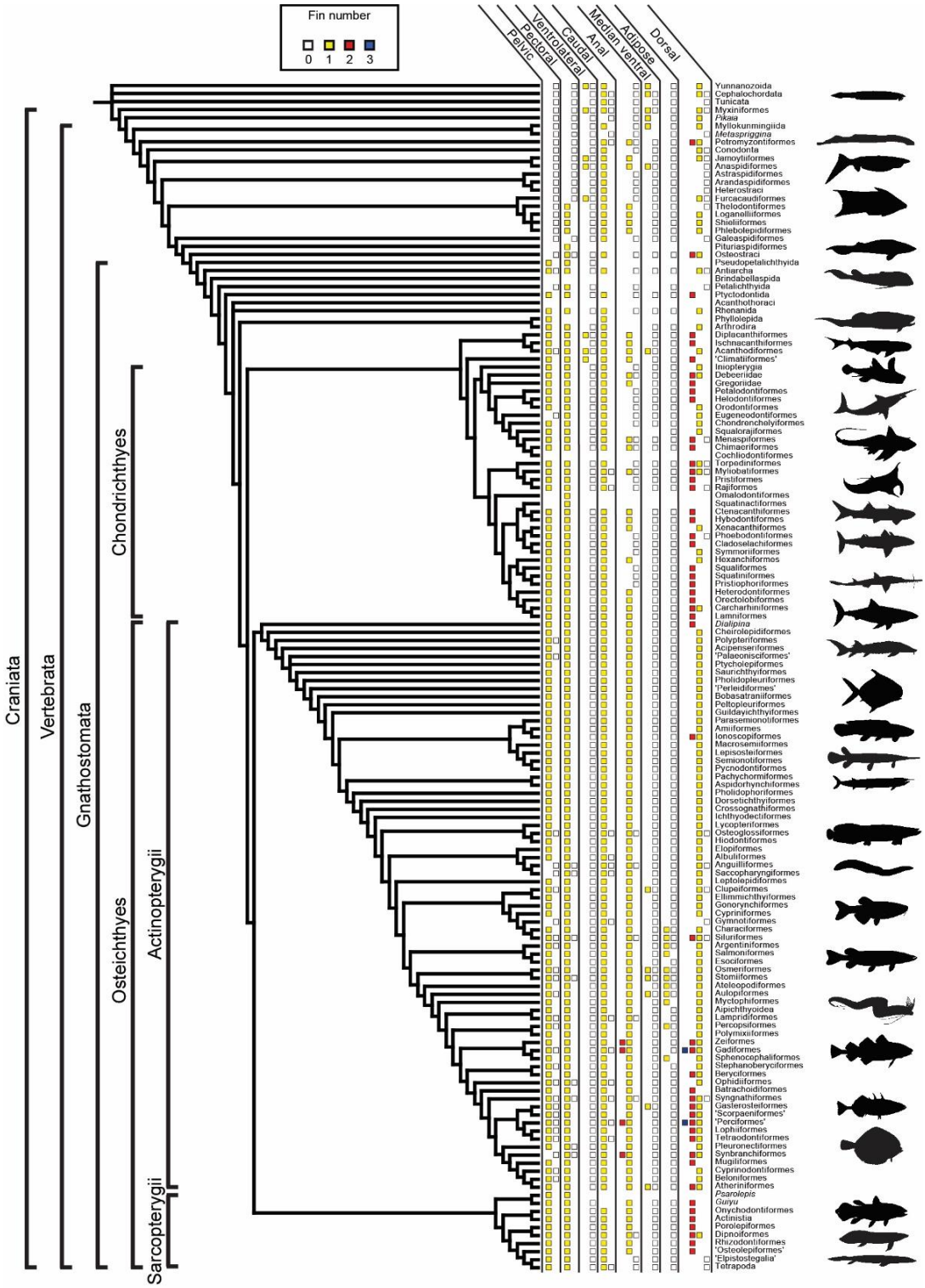
Fin number
0 1 2 3
Pelvic
Pectoral
Ventrolateral
Caudal
Anal
Median ventral
Adipose
Dorsal
Craniata
Vertebrata
Gnathostomata
Chondrichthyes
Osteichthyes
Actinopterygii
Sarcopterygii
Yunnanozoida
Cephalochordata
Tunicata
Myxiniformes
Pikaia
Myllokunmingiida
Metaspriggina
Petromyzontiformes
Conodonta
Jamoytiiformes
Anaspidiformes
Astraspidiformes
Arandaspidiformes
Heterostraci
Furcacaudiformes
Thelodontiformes
Loganelliiformes
Shieliiformes
Phlebolepidiformes
Galeaspidiformes
Pituriaspidiformes
Osteostraci
Pseudopetalichthyida
Antiarcha
Brindabellaspida
Petalichthyida
Ptyctodontida
Acanthothoraci
Rhenanida
Phyllolepida
Arthrodira
Diplacanthiformes
Ischnacanthiformes
Acanthodiformes
'Climatiiformes'
Iniopterygia
Debeeriidae
Gregoriidae
Petalodontiformes
Helodontiformes
Orodontiformes
Eugeneodontiformes
Chondrenchelyiformes
Squalorajiformes
Menaspiformes
Chimaeriformes
Cochliodontiformes
Torpediniformes
Myliobatiformes
Pristiformes
Rajiformes
Omalodontiformes
Squatinactiformes
Ctenacanthiformes
Hybodontiformes
Xenacanthiformes
Phoebodontiformes
Cladoselachiformes
Symmoriiformes
Hexanchiformes
Squaliformes
Squatiniformes
Pristiophoriformes
Heterodontiformes
Orectolobiformes
Carcharhiniformes
Lamniformes
Dialipina
Cheirolepidiformes
Polypteriformes
Acipenseriformes
'Palaeonisciformes'
Ptycholepiformes
Saurichthyiformes
Pholidopleuriformes
'Perleidiformes'
Bobasatraniiformes
Peltopleuriformes
Guildayichthyiformes
Parasemionotiformes
Amiiformes
Ionoscopiformes
Macrosemiiformes
Lepisosteiformes
Semionotiformes
Pycnodontiformes
Pachychormiformes
Aspidorhynchiformes
Pholidophoriformes
Dorsetichthyiformes
Crossognathiformes
Ichthyodectiformes
Lycopteriformes
Osteoglossiformes
Hiodontiformes
Elopiformes
Albuliformes
Anguilliformes
Saccopharyngiformes
Leptolepidiformes
Clupeiformes
Ellimmichthyiformes
Gonorynchiformes
Cypriniformes
Gymnotiformes
Characiformes
Siluriformes
Argentiniformes
Salmoniformes
Esociformes
Osmeriformes
Stomiiformes
Ateleopodiformes
Aulopiformes
Myctophiformes
Aipichthyoidea
Lampridiformes
Percopsiformes
Polymixiiformes
Zeiformes
Gadiformes
Sphenocophaliformes
Stephanoberycitformes
Beryciformes
Ophidiiformes
Batrachoidiformes
Syngnathiformes
Gasterosteiformes
'Scorpaeniformes'
'Perciformes'
Lophiiformes
Tetraodontiformes
Pleuronectiformes
Synbranchiformes
Mugiliformes
Cyprinodontiformes
Beloniformes
Atherinifomes
Psarolepis
Guiyu
Onychodontiformes
Actinistia
Porolepiformes
Dipnoiformes
Rhizodontiformes
'Osteolepiformes'
'Elpistostegalia'
Tetrapoda

Figure 6: Distribution of fin conditions on the supertree of fishes showing the interrelationships among extant and extinct orders of fishes. Some non-ordinal ranked taxa that were included in the supertree analysis have been pruned for simplification. Colored squares above terminal branches represent sampled fin character states for each order/subgroup.

Multiple correspondence analyses were performed using the ca package (Nenadic and Greenacre 2007), and Spearman's rank correlations were calculated with the Hmisc package (Harrell 2016) in R version 3.2.4 (R Core Team 2016).

1.5 Results

1.5.1 Fish supertree

The phylogenetic supertree analysis summarizes the topologies of 17 source trees for agnathans, 13 trees for basal gnathostomes (placoderms and acanthodians), 24 trees for chondrichthyans, 39 trees for actinopterygians and 25 trees for sarcopterygians. The supertree generated using Nixon's parsimony ratchet and 50% majority rule consensus contains 163 terminal branches and 156 internal nodes, making it 96.3% resolved compared to a fully dichotomous phylogenetic tree. The strict consensus tree contains 142 internal nodes making it 87.6% resolved. The single most parsimonious solution using the optimum parsimony setting generated a tree with 160 internal nodes, making it 98.8% resolved. We used a pruned version of the 50% majority rule supertree for the mapping of fin characters (Figure 6). The strict consensus and the optimum parsimony solutions can be found in Annexe C.

To our knowledge, this is the first time an attempt has been made to reconcile such a large number of fish orders within a single supertree using modern phylogenetic methods. Most recently published trees with broad taxonomic scopes have focused on interrelationships among agnathans, basal gnathostomes, or derived actinopterygians

(Percomorpha). The phylogenetic relationships of basal vertebrates, particularly the interrelationships of fossil taxa, have been debated for many years (see Annexe C). Among these contentious groups, our consensus topology, generated from recent phylogenetic analyses, posits that living agnathans are paraphyletic, thelodonts are monophyletic, placoderms are stem gnathostomes, and acanthodians are stem chondrichthyans.

Among chondrichthyans, actinopterygians and sarcopterygians, the supertree analysis recovered most ordinal groupings that have generally been recognized as clades (e.g., Euchondrocephali, Elasmobranchii, Squalomorphii, Galeomorphii, Osteoglossomorpha, Elopomorpha, Otocephala, Acanthomorpha, Tetrapodomorpha). A notable exception occurred when performing the analysis for chondrichthyans. In a first run of the supertree analysis with batoids represented as four separate orders, the resulting trees showed an unusual topology where batoids were polyphyletic and variously distributed among Paleozoic elasmobranchs. We subsequently ran the analysis with "Batoidea" as a terminal branch, thus enforcing the known monophyly of the group, and obtained the topology presented in Figure 2, where batoids are placed as the most basal of the Elasmobranchii. Although some have suggested that batoids are highly derived selachians (e.g., Shirai 1992; de Carvalho 1996; de Carvalho and Maisey 1996; Shirai 1996), a more recent view which is well supported by molecular-based phylogenies is that batoids are an elasmobranch clade that shares a common ancestor with the Selachii (Compagno 1973, 1977; Douady et al. 2003; Vélez-Zuazo and Agnarsson 2011; Naylor et al. 2012). Yet in this case, the supertree approach failed to retrieve this topology. The inconsistency in the placement of the batoids can likely be imparted to two issues in our dataset of phylogenetic trees. The first issue is described as the "rogue branch" problem in Ragan (1992), whereby a single branch appears at radically different places in the trees considered. The second issue is that batoids are only rarely incorporated in datasets focusing on fossil chondrichthyans. This results in the Paleozoic elasmobranchs being resolved as stem euselachians. The

batoids are most likely pulled further towards the stem because chimaeras are incorporated in analyses focusing on the interrelationships of extant chondrichthyans, and that in these analyses batoids are most frequently resolved as basal to other elasmobranchs.

1.5.2 Mapping the evolutionary history of fish appendages

The mapping of the presence/absence data on the supertree (Figure 6) allows us (1) to visually establish where most of the morphological disparity occurs within the phylogeny (2) and infer the order of appearance of each of the fins. There are three sections of the phylogeny where most of the disparity in fin configurations is concentrated: (1) agnathans, (2) chondrichthyans and (3) derived actinopterygians. The disparity in agnathans is largely due to the original diversification of fin configurations and the sequential addition of novel fins within this paraphyletic assemblage of basal fishes, while the disparity in chondrichthyans and actinopterygians results mostly from fin losses, duplications of preexisting fins, or the addition of new fins.

1.5.2.1 *Agnathans*

With the exception of the pelvic and adipose fins, most fins appear early during the evolutionary history of fishes. Median fins are already present along the dorsal and ventral midline even in the most basal craniates and vertebrates (e.g., *Haïkouella*, *Myllokunmingia*, *Haikouichthys*). The fin which extends along the ventral midline in these forms is positioned anteriorly to the anus and as such does not qualify as an anal fin. This fin configuration is reminiscent of what is observed in cephalochordates, although in the latter case, the dorsal finfold extends further anteriorly reaching the tip of the notochord where it forms the "rostral fin." In *Haïkouella* and *Haikouichthys*, the median fins are continuous around the tail where they form a rudimentary caudal fin. A well-developed caudal fin is a generalized feature of all other agnathan taxa with the

exception of a few hagfishes and lampreys. The presence of a caudal fin early in the evolutionary history of fishes is expected considering that a post-anal tail is a chordate synapomorphy: even tunicates possess a caudal fin prior to metamorphosis (Lemaire 2011). An anal fin is present in a few Carboniferous lampreys and becomes a common feature among anaspids and thelodonts.

Paired fins also arise among agnathans. Paired fins first occur as long-based ribbon-like fins, such as in anaspids. In osteostracans and some thelodonts, the paired fins are shorter-based and have a position comparable to that of pectoral fins, although homology to the pectoral fins of gnathostomes is currently only proposed for osteostracan paired fins.

The disparity in fin configurations within agnathans is predominantly due to differences among taxa as to the presence or absence of the median and paired fins as they successively appear during the evolutionary history of these early fishes, generating novel combinations in different groups. A few taxa also possess two dorsal fins, a condition which seems to have evolved independently in lampreys and osteostracans. Based on the number of character changes on the supertree, the presence/absence of the dorsal and anal fins seem to be the most important source of disparity in fin configurations in agnathans, followed by the median ventral fin and ventrolateral paired fins.

1.5.2.2 *Chondrichthyans*

In chondrichthyans, some fins contribute very little to the disparity in fin configurations: the pectoral fins are always present, the pelvic fins are lost only in the Eugeneodontiformes, and the caudal fin is always present, except in Myliobatiformes where it is generally absent and in Rajiformes where it is occasionally absent. Most of the disparity in fin configurations relates to the dorsal and anal fins. The majority of

chondrichthyans have one or two dorsal fins, although some forms are characterized by the absence of this fin (e.g., some Rajiformes, Torpediniformes and Myliobatiformes). Absence of the anal fin is much more frequent than that of the dorsal fin, particularly among batoids, squalomorphs and holocephalans: the anal fin is lacking in at least some representatives of 18 chondrichthyan orders, whereas the dorsal fin is lacking in some representatives of only five orders.

1.5.2.3 *Actinopterygians*

Basal actinopterygians show very little disparity in their fin configurations: they generally have single dorsal, anal and caudal fins, and paired pectoral fins. The only source of disparity concerns the occasional loss of the pelvic fins, and the presence of two dorsal fins in *Dialipina salgueiroensis* (Schultze and Cumbaa 2001) and *Placidichthys bidorsalis* (Brito 2000). The second dorsal fin in *Dialipina* supports the hypothesis that the plesiomorphic condition for basal gnathostomes might have been the presence of two dorsal fins (Janvier 1996b; Schultze and Cumbaa 2001; Hanke 2002; Cloutier and Arratia 2004), whereas the presence of two dorsal fins in *Placidichthys* is secondarily derived.

In contrast, derived actinopterygians are much more disparate in their fin configurations. Part of this disparity can be accounted for by repeated losses of some of the fins. Indeed, any of the median and paired fins, including the caudal fin, can be lacking in some actinopterygian groups. The pelvic fins are the most frequently lost: they are reported as absent in representatives of 25 orders from our dataset. Comparatively, only ten orders contain species that lack a caudal fin, seven orders contain species that lack pectoral fins, six orders contain species that lack the dorsal fin and six orders contain species that lack an anal fin. The disparity among derived actinopterygians can also be explained partly by apparent duplications of the median fins. Derived actinopterygians, more specifically the Acanthomorpha, frequently

possess more than one dorsal and/or anal fins: 13 actinopterygian orders contain species that have at least two separate dorsal fins, and four of these orders contain species that also have two anal fins. Furthermore, some species of two acanthomorph orders even show three separate dorsal fins. Yet another source of disparity in actinopterygians is brought about by the addition of novel fins. The adipose fin is considered as such an evolutionary novelty (Stewart and Hale 2013; Stewart et al. 2014) which first appears among the Ostariophysi. An adipose fin is present in representatives of 11 actinopterygian orders from our dataset. In some of these groups, it is occasionally combined to a median ventral fin positioned anteriorly to the anal fin (referred to as a ventral adipose fin in morphological descriptions), although this ventral fin can be present even if the dorsal adipose fin is absent. A median ventral fin is found in some species of six of the orders sampled in our actinopterygian dataset.

1.5.2.4 *Sarcopterygians*

Sarcopterygians display far less disparity in their fin configurations: differences among taxa are limited to the number of dorsal fins, and the presence/absence of the dorsal, anal and caudal fins. Furthermore, only two orders (Dipnoiformes and "Elpistostegalia") show some disparity in fin configurations among the species they contain. Most sarcopterygians have two dorsal fins, a single anal fin, a caudal fin, and paired pectoral and pelvic fins. The Dipnoiformes are the most disparate order in terms of fin configurations: there can be either one or two dorsal fins, and a separate anal fin is lost in derived dipnoans. Elpistostegalians, the most derived piscine tetrapodomorphs, are characterized by the loss of the dorsal and anal fins although the caudal fin remains. The paired fins are conserved in all sarcopterygian taxa, including tetrapods where they evolved towards the fore- and hindlimbs (Ahlberg 1989; Janvier 1996b; Shubin et al. 1997; Coates and Cohn 1998; Coates et al. 2002; Shubin 2002; Daeschler et al. 2006; Shubin et al. 2006; Shubin et al. 2009).

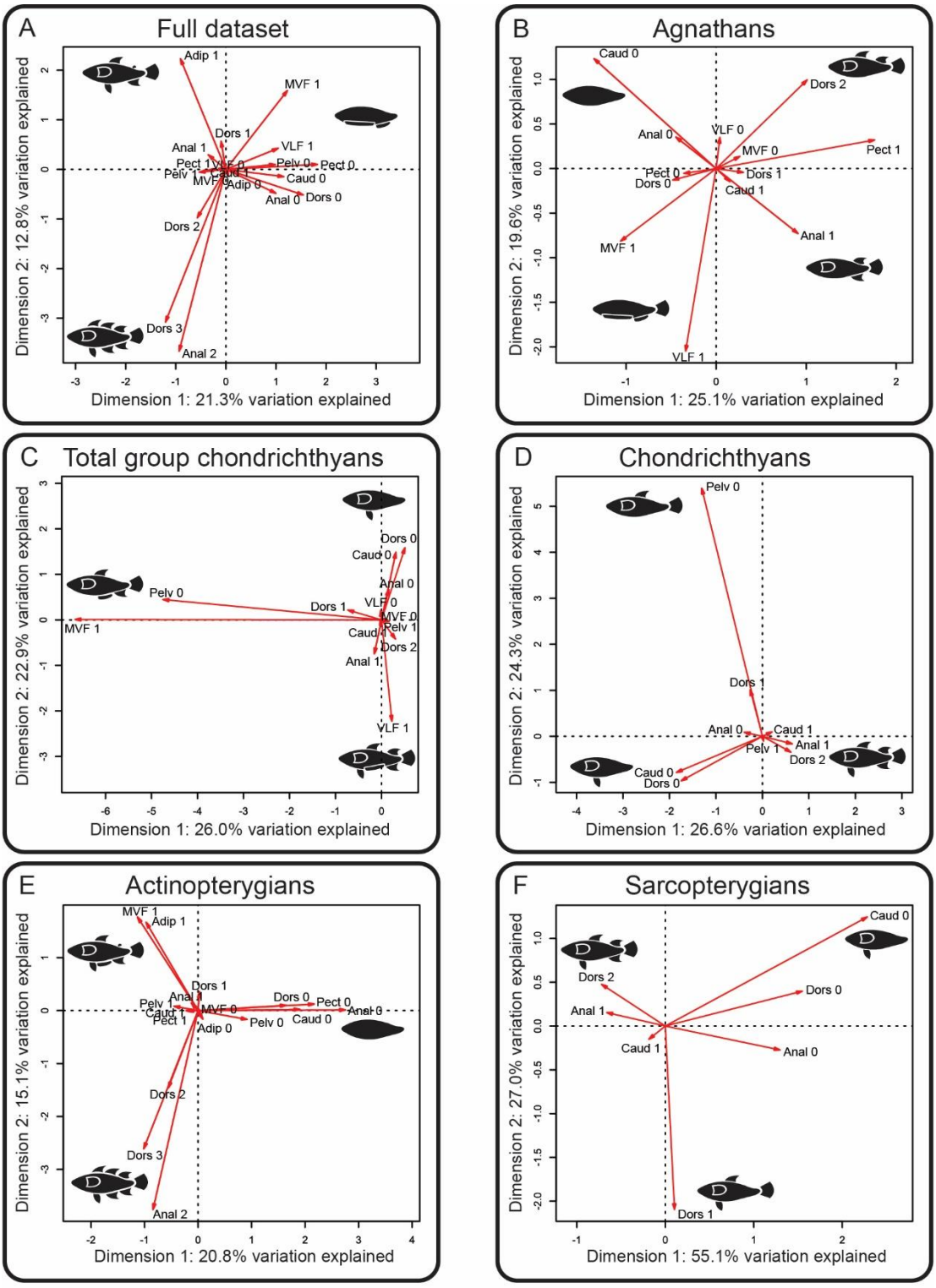
A
Full dataset
Dimension 2: 12.8% variation explained
Dimension 1: 21.3% variation explained
Adip 1
MVF 1
Dors 1
Anal 1
VLF 1
Pect 1
Pelv 0
Pect 0
Pelv 1
Caud 0
MVF 0
Adip 0
Anal 0
Dors 0
Dors 2
Dors 3
Anal 2
B
Agnathans
Dimension 2: 19.6% variation explained
Dimension 1: 25.1% variation explained
Caud 0
Dors 2
Anal 0
VLF 0
MVF 0
Pect 1
Pect 0
Dors 1
Dors 0
Caud 1
Anal 1
MVF 1
VLF 1
C
Total group chondrichthyans
Dimension 2: 22.9% variation explained
Dimension 1: 26.0% variation explained
Dors 0
Caud 0
Anal 0
Pelv 0
Dors 1
VLF 0
MVF 0
MVF 1
Pelv 1
Caud 1
Dors 2
Anal 1
VLF 1
D
Chondrichthyans
Dimension 2: 24.3% variation explained
Dimension 1: 26.6% variation explained
Pelv 0
Dors 1
Anal 0
Caud 1
Pelv 1
Anal 1
Dors 2
Caud 0
Dors 0
E
Actinopterygians
Dimension 2: 15.1% variation explained
Dimension 1: 20.8% variation explained
MVF 1
Adip 1
Dors 1
Anal 1
Pelv 1
Caud 1
Pect 1
MVF 0
Dors 0
Pect 0
Anal 0
Pelv 0
Caud 0
Adip 0
Dors 2
Dors 3
Anal 2
F
Sarcopterygians
Dimension 2: 27.0% variation explained
Dimension 1: 55.1% variation explained
Caud 0
Dors 2
Dors 0
Anal 1
Caud 1
Anal 0
Dors 1

Figure 7: Biplots of the multiple correspondence analyses. Lettered panels represent the results for (A) the entire dataset, (B) agnathans, (C) chondrichthyans, (D) total-group chondrichthyans, (E) actinopterygians and (F) sarcopterygians. Fish silhouettes represent the major trends in fin configurations among each groups.

1.5.3 Covariation in the presence/absence of fish appendages

Multiple correspondence analyses were performed with the complete dataset (147 orders) and also on six subsets of the data corresponding to major taxonomic groups [i.e., agnathans (18 orders), total group chondrichthyans (37 orders), chondrichthyans excluding acanthodian-like taxa (33 orders), actinopterygians (73 orders) and sarcopterygians (7 orders)], most of which are monophyletic with the exception of agnathans. We found that the removal of taxa with missing data was for the most part inconsequential, affecting only the percentage of variance explained by the major axes of variation. As such, we focus on the results incorporating the entire dataset (Figure 7). We limited our analysis to the first two dimensions of the MCAs because additional dimensions showed increasingly rare fin combinations in the dataset and were not biologically interpretable.

The first two dimensions of the MCA on the entire dataset (Figure 7A) explain 21.3% and 12.8% of the variation, respectively. The first dimension contrasts fishes bearing only median ventral fins and/or ventrolateral paired fins, to fishes that have two or three dorsal and anal fins, or an adipose fin. This can be interpreted as contrasting patterns of fin configurations found in basal agnathans to those of acanthomorphs. The second dimension contrasts fishes bearing an adipose fin and a median ventral fin to those that have two (or three) dorsal and anal fins. An adipose fin is commonly found in a number of orders of basal eutelosteans, whereas the presence of three dorsal fins and two anal fins is only found in the more advanced euteleosteans (Acanthomorpha). Additionally, based on the acute angles between some vectors and similarities in their relative

lengths, there is evidence for coordinated losses or duplications between some of the fins. This is observed for the coordinated duplications (or triplications) of the dorsal and anal fins, as well as for the coordinated losses of the dorsal and anal fins, and of the pectoral and pelvic fins.

The first two dimensions of the MCA on agnathans (Figure 7B) explains 25.1% and 19.6% of the variation, respectively. The first dimension contrasts fishes that have caudal, dorsal, anal and pectoral fins to those that do not have these fins. The former pattern is found in the more basal agnathans that have long-based ribbon-like median and paired fins, while the latter fin configuration is characteristic of fishes close to the agnathan-gnathostome transition, such as the osteostracans. The second dimension contrasts primarily a morphology where most fins are absent with the exception of two dorsal fins, a pattern found in a single petromyzontid fossil species, to forms where there is a single copy of each fin. The angles between the vectors for each of the fins are relatively equal, resulting in a star-shaped pattern: this suggests that there is little covariation among the fins and that they are all independent from one another. Alternatively, this star-shaped pattern could also partly result from the difficulties in correctly identifying homologies in fin characters among agnathans. It has been suggested for example that the paired fins of some anaspids could be homologous to the pelvic fins of gnathostomes (Wilson et al. 2007).

For the total group chondrichthyans (i.e., including acanthodians and putative chondrichthyans) (Figure 7C), the first two dimensions of the MCA explain 26.0% and 22.9% of the variation, respectively. The first dimension contrasts forms that have a single dorsal fin, no pelvic fins and a median ventral fin, to fishes that have lost their median fins and/or have two dorsal fins. This can be interpreted as opposing the morphology of a single genus of acanthodians, *Acanthodes*, to the disparity in batoid morphologies. The second dimension opposes forms that have ventrolateral paired fins, an anal fin and two dorsal fins, to forms that have lost their median fins. This opposes

a morphology found in climatiid and diplacanthid acanthodians to the loss of median fins found in some batoids, more specifically among the Rajiformes and Myliobatiformes. As with the analysis on the full dataset, the relative lengths and angles between some of the vectors show coordinated patterns between some of the fins, in this case suggesting coordinated losses of the dorsal, anal and caudal fins.

In the analysis restricted to undoubted chondrichthyans (Figure 7D), the first two dimensions of the MCA explain 26.6% and 24.3% of the variation, respectively. The first dimension contrasts forms that have lost most of their median fins and the pelvic fins, to morphologies where all of the fins are present including two dorsal fins. The latter pattern is characteristic of the shark-like neoselachians, while the former seems to be a combination of characters found either in batoids or in the Eugeneodontiformes. The second axis primarily contrasts forms that have lost the pelvic fins and have a single dorsal fin, to those that have lost the dorsal and caudal fins or have two dorsal fins. As such, this dimension of the MCA opposes the Eugeneodontiformes, the only chondrichthyan taxon where the pelvic fins are absent, to the disparity patterns of other chondrichthyans.

In actinopterygians, the first two dimensions of the MCA (Figure 7E) explain 20.8% and 15.1% of the total variation, respectively. The first dimension contrasts forms that have lost all of their fins, to morphologies with additional fins. These accessory fins correspond either to the addition of second and third dorsal and anal fins, or to the addition of median ventral fins and adipose fins. The loss of all fins is rare and can be found only in a few Anguilliformes and Gasterosteiformes, generally associated with an elongated body shape. The pattern with supplementary fins is characteristic of the more advanced teleosteans (Ostariophysi and Euteleostei). The second dimension opposes forms where a preanal median fold and an adipose fin are present to forms with serial duplications of the dorsal and anal fins. This contrasts two ways by which additional median fins can be added to the body, the first being characteristic of basal

euteleosts while the latter is characteristic of the acanthomorphs. As with the analysis focusing on the full dataset, the angles and lengths of the vectors suggest coordinated patterns of loss and duplication among fins. Again, the presence of additional dorsal and anal fins appear coordinated. The presence of a median ventral fin and of an adipose fin also seems to be coordinated. However, as opposed to the results from the full dataset, here the acute angles between vectors representing fin losses suggest coordinated losses that affect all median and paired fins at once.

In sarcopterygians, the first two dimensions of the MCA (Figure 7F) explain 55.1% and 27.0% of the variation, respectively. The disparity in fin configurations is limited to the number of dorsal fins and the presence/absence of the dorsal, anal and caudal fins. Pectoral and pelvic fins are always present in sarcopterygians. The first axis contrasts fishes bearing a caudal, an anal, and two dorsal fins to forms that have lost all of their median fins. Essentially, this contrasts most piscine sarcopterygians to tetrapods. The second axis contrasts forms that have a single dorsal fin and no anal fin, to forms that have either two dorsal fins, or where the dorsal and the caudal fin are both absent. This contrasts the derived condition found in dipnoans to a combination of fin characters that is a composite of the other sarcopterygians. As opposed to the results for most of the other analyses, the angles and relative lengths of the vectors from this analysis do not suggest any particularly strong relationships between any of the variables.

MCAs were also performed for the complete gnathostome dataset (125 orders) and the complete osteichthyan dataset (80 orders) (see Annexe E). The overwhelming actinopterygian pattern was pervasive in both of these analyses, particularly for the osteichthyan dataset. This is not unexpected since the ordinal diversity and morphological disparity in actinopterygians by far exceeds that of the other gnathostome groups.

Table 3: *P*-values of Fisher's exact test between fins. The dataset comprises all possible fin configurations for each order, and includes rows with missing data.

	median ventral fin	ventro-lateral paired fins	pectoral fins	pelvic fins	dorsal fins	adipose fin	anal fins
ventro-lateral paired fins	0.022						
pectoral fins	4.53e-04	0.007					
pelvic fins	0.016	0.354	2.2e-16				
dorsal fins	0.235	0.255	3.50e-09	9.41e-08			
adipose fin	0.052	1	0.083	0.002	0.036		
anal fins	0.172	1	7.94e-09	0.005	2.01e-12	0.021	
caudal fin	1	0.607	0.007	2.00e-04	0.013	0.382	0.011

Fisher's exact test was used to identify sets of fins that display non-random patterns in their presence/absence, which would be congruent with a modular organization. In other words, if two fins are part of the same fin module, we expect that coordination in their character states (presence, absence or duplication) should be more frequently observed. Spearman's rank correlations was used to determine if the significant relationships between pairs of fins revealed by the chi-squared test is due to covariation in the presence/absence data, or from antagonistic relationships (one fin is present while the other is absent). In the analysis where unique fin combinations were identified for each individual order, a number of pairs of fins showed non-random patterns in

Table 4: Spearman's rank correlation coefficients between fins (below diagonal) and associated *p*-values (above diagonal). The dataset comprises all possible fin configurations for each order, and includes rows with missing data. Sample sizes vary between 281 and 293 among pairwise comparisons because of missing data. Significant results are in bold.

	median ventral fin	ventro-lateral paired fins	pectoral fins	pelvic fins	dorsal fins	adipose fin	anal fins	caudal fin
median ventral fin		0.002	<0.0001	0.008	0.087	0.019	0.047	0.583
ventro-lateral paired fins	**0.18**		0.002	0.265	0.942	0.451	0.957	0.271
pectoral fins	**-0.24**	**-0.18**		<0.0001	<0.0001	0.071	<0.0001	0.002
pelvic fins	**-0.16**	-0.07	**0.57**		<0.0001	0.003	0.002	<0.0001
dorsal fins	-0.10	0.00	**0.36**	**0.34**		0.194	<0.0001	0.001
adipose fin	**0.14**	-0.04	0.11	**0.17**	-0.08		0.027	0.171
anal fins	**-0.12**	0.00	**0.37**	**0.18**	**0.28**	**0.13**		0.002
caudal fin	0.03	0.07	**0.18**	**0.23**	**0.19**	0.08	**0.19**	

their co-occurrence (Tables 3 and 4). Highly significant results were obtained for the following fin pairs using Fisher's exact test: median ventral/pectoral, ventrolateral paired/pectoral, pectoral/pelvic, pectoral/dorsal, pectoral/anal, pectoral/caudal,

Table 5 : *P*-values of Fisher's exact test between types of fins. The dataset comprises each unique combination of character states within the entire dataset. Rows with missing data were excluded.

	median ventral fin	ventro-lateral paired fins	pectoral fins	pelvic fins	dorsal fins	adipose fin	anal fins
ventro-lateral paired fins	0.592						
pectoral fins	0.249	0.082					
pelvic fins	0.488	0.436	2.16e-05				
dorsal fins	0.762	0.828	0.300	0.259			
adipose fin	0.449	1	0.544	0.085	0.810		
anal fins	1	0.798	0.142	0.206	0.140	0382	
caudal fin	0.417	0.170	0.750	1	0.775	0.561	0.430

pelvic/dorsal, pelvic/adipose, pelvic/anal, pelvic/caudal and dorsal/anal fins. All of these pairs of fins were shown to be concurrently present or absent, with the exception of the median ventral/pectoral and the ventrolateral paired/pectoral fins, which display opposite trends in their presence/absence data. Significant results were obtained for the median ventral/ventrolateral paired, median ventral/pelvic, dorsal/adipose, dorsal/caudal, anal/adipose and anal/caudal fins. The median ventral/ventrolateral paired, dorsal/caudal, anal/adipose and anal/caudal fins co-occur or are jointly absent, whereas the median ventral/pelvic, ventrolateral paired/pectoral and dorsal/adipose fins vary in opposite directions.

Table 6: Spearman's rank correlation coefficients between types of fins (below diagonal) and associated *p*-values (above diagonal). The dataset comprises each unique combination of character states within the entire dataset. Rows with missing data were excluded (N = 51). Significant results are in bold.

	median ventral fin	ventro-lateral paired fins	pectoral fins	pelvic fins	dorsal fins	adipose fin	anal fins	caudal fin
median ventral fin		0.425	0.168	0.445	0.376	0.473	0.589	0.285
ventro-lateral paired fins	0.11		0.032	0.354	0.312	0.486	0.724	0.099
pectoral fins	-0.20	**-0.30**		<0.0001	0.069	0.195	0.050	0.700
pelvic fins	-0.11	-0.13	**0.59**		0.083	0.050	0.076	0.931
dorsal fins	-0.13	-0.14	0.26	0.25		0.474	0.095	0.446
adipose fin	0.10	-0.10	0.18	0.28	-0.10		0.250	0.306
anal fins	-0.08	0.05	0.28	0.25	0.24	0.16		0.160
caudal fin	0.15	0.23	-0.06	-0.01	0.11	0.15	0.20	

The simplification of the dataset to identify every possible fin combinations resulted in 51 unique combinations out of a total of 768 possibilities. Fisher's exact test (Table 5) identified a single pair of fins, the pectoral/pelvic fins, as highly statistically significant (p = 2.16e-05). The pectoral and pelvic fins were shown to be concurrent in their

presence or absence by the results of Spearman's rank correlations (Table 6). Using this dataset, the dorsal/anal fins pair was not found to be statistically significant (p = 0.140). Both the pectoral/ventrolateral paired fins (p = 0.082) and the pelvic/adipose fins (p = 0.085) are marginally non-significant statistically. Based on Spearman's rank correlations, the pectoral and ventrolateral paired fins were found to vary in opposite direction, whereas the pelvic and adipose fins showed coordination in their presence/absence.

1.6 Discussion

For the first time, we have an integrative picture of the evolution of fin configurations and covariation patterns of these appendages among a large diversity of lower vertebrates. The two objectives of this paper were (1) to examine the morphological disparity in fin configurations among basal vertebrates and gain insight into the sequential appearance of median and paired fins in fishes, and (2) to investigate macroevolutionary patterns of co-occurrence among some of the fins, which could then be interpreted as evolutionary modules. These two objectives are not independent. The evolutionary emergence of novel fins could involve the duplication or co-option of pre-existing fin modules. Such scenarios have already been proposed, whether or not explicitly, in the context of the evolution of paired fins in early vertebrates (Freitas et al. 2006; Freitas et al. 2014), the pectoral and pelvic fins in gnathostomes (Shubin et al. 1997), the spine-brush-complex in symmoriiform sharks (Maisey 2009), the adipose fin in euteleosts (Stewart and Hale 2013; Stewart et al. 2014; Stewart 2015), and the spinous dorsal fin in acanthomorphs (Mabee et al. 2002). Modularity also promotes functional and morphological disparity, because modules can be individually optimized without affecting other parts of an organism (Wagner 1996; Wagner and Altenberg 1996; Hansen 2003; Hansen et al. 2003). Thus, a modular organization of appendages is useful to explain the disparity of fin configurations in fishes, but also at a larger scale of limbs in all vertebrates. The paired appendages of tetrapods provide a

very telling example: the fore- and hindlimbs can be modified independently, which was a necessary prerequisite for the evolution of specialized structures, such as the wings in birds or bats (Shubin et al. 1997; Hall 2010).

1.6.1 Disparity in fin configurations

The mapping of fin characters on the supertree reveals which groups are the most disparate in their fin configurations: agnathans, chondrichthyans and derived actinopterygians display the greatest disparity in fin configurations, although they differ as to which fins are responsible for generating this disparity. Among agnathans, new fins are sequentially added and long ribbon-like fins are gradually replaced by more spatially constricted median and paired fins. Thus, the disparity in this part of the tree results from tinkering with fin configurations and building towards the gnathostome Baüplan. In chondrichthyans, the most important source of disparity is the loss of some (occasionally all) of the median fins. The most disparate fin combinations are found among teleosteans, owing to frequent losses affecting median and/or paired fins, additions of novel fins, or duplications of preexisting fins.

In agnathans, all of the fins (with the exception of the adipose and pelvic fins that are absent) participate in the observed patterns of disparity in fin configurations. Much of this disparity can be accounted for by the gradual modification of long-based median and paired ventrolateral finfolds into shorter-based dorsal, anal and pectoral fins. Absence of the caudal fin also stands out as a source of disparity, yet this is restricted to a few species of hagfishes and lampreys. Among these, two extinct species, the putative hagfish *Gilpichthys greenei* and the putative lamprey *Pipiscius zangerli*, might in fact represent larval organisms (Bardack and Richardson 1977; Bardack 1998). As such the specimens assigned to these two taxa might not represent adult morphologies and the scoring of characters could have differed in metamorphosed specimens. In extant species, the caudal fin is generally present although it can be vestigial or even

absent [e.g., *Myxine formosana* (Mok and Kuo 2001; McMillan and Wisner 2004)]. As for the paired fins, ventrolateral paired fins are variably present among anaspids and thelodonts, while shorter-based paired fins that have a position reminiscent of gnathostome pectoral fins are found in some thelodonts and in the osteostracans.

The disparity in fin configurations that is observed among chondrichthyans can appear surprising given only the modern forms. Paleozoic chondrichthyans, however, present highly disparate morphologies, comparatively making modern holocephalans and elasmobranchs seem conservative (Zangerl 1981; Maisey 1986; Stahl 1999; Grogan et al. 2012; Gess and Coates 2015). Most of the disparity in fin configurations for chondrichthyans can be accounted for by changes as to the number of median fins that are present. The anal fin is lost in representatives of numerous chondrichthyan orders. Contrastingly, most chondrichthyans have two dorsal fins, although the presence of a single dorsal fin is also common. The dorsal fin is lacking only in a few chondrichthyan taxa. There is also some disparity due to the occasional loss of the caudal fin in some batoids. Batoids are characterized by dorso-ventrally flattened bodies, greatly enlarged pectoral fins and in many species, a long whip-like tail. Propulsion in most of these forms is achieved through undulations (e.g., most skates and sting rays) or oscillations (e.g., eagle rays) of the widened pectoral fins (Rosenberger 2001; Schaefer and Summers 2005; Franklin et al. 2014), which provides a functional context for the loss of the caudal fin when compared to most other chondrichthyans that use a caudal fin-based propulsion. The paired fins do not account for much of the disparity in fin configurations: absence of the pelvic fins is limited to representatives of a single order of extinct chondrichthyans, the Eugeneodontiformes.

In derived actinopterygians, an important part of the disparity in fin configurations relates to the presence/absence of the pelvic fins, and to the number of dorsal fins. Pectoral fins are lost far less frequently than the pelvic fins. For instance in teleosteans, the loss of pelvic fins has been reported in over 100 families belonging to 20 different

orders (Yamanoue et al. 2010), whereas the loss of pectoral fins is reported for only eight teleostean orders in our dataset. The more frequent loss of the pelvic fins could reflect their lesser functional importance for swimming, when compared to the pectoral fins (Harris 1936, 1938; Lindsey 1978; Yamanoue et al. 2010). In the smooth dogfish (*Mustelus canis*), experiments on fin amputations have shown that the sharks are able to correct for the loss of the pelvic fins using their other median and paired fins (Harris 1936). Contrastingly, Standen (2008) showed that in the rainbow trout (*Oncorhynchus mykiss*), the pelvic fins accomplish complex motions, indicating that their functional importance might have been underestimated. From an eco-morphological perspective, loss of the pelvic fins is often seen in fishes that possess an elongated body shape and occupy complex habitats such as coral reefs or crevices (Rade and Ward 2010; Ward and Mehta 2010; Yamanoue et al. 2010). In these elongated fishes, the pectoral fins are often reduced as well, while the median fins are expanded in length and confluent with the caudal fin (Ward and Mehta 2010). In tetrapods, limb reduction and body elongation is often associated with fossorial or semi-fossorial organisms (Gans 1975; Withers 1981; Adriaens et al. 2002). Thus, in structure-rich habitats, the presence of paired lateral appendages could be disadvantageous, particularly for burrowers or parasitic fishes (Hollò and Novàk 2012). Additionally, some of these elongated fishes use anguilliform locomotion, which involves undulations along the entire body length, and less emphasis on the use of the paired fins for propulsion (Webb 1975; Lindsey 1978). From a macroevolutionary perspective, another hypothesis to explain that the pelvic fins are more frequently lost than the pectoral fins is that pelvic fins appeared after the pectoral fins during the evolutionary history of fishes (Coates 1994, 2003). Additionally, from a developmental perspective, pectoral fins develop prior to the pelvic fins (Faustino and Power 1999; Joss and Longhurst 2001). It has been observed that the last structures to appear also tend to be the first to be lost through paedomorphosis (Britz and Conway 2009). For instance, in reptiles and lissamphibians, patterns of limb reduction reflect developmental sequences: the digits that develop last are the first to be lost in species with reduced limbs (Gans 1975; Shubin 2002).

Although the pelvic fins are frequently lost independently from the pectoral fins, the converse is rare. Excluding agnathans where girdle-supported pelvic fins have not yet appeared, in seven of the eight actinopterygian orders where the pectoral fins are occasionally lost, the pelvic fins also tend to be absent. In fact, the loss of pectoral fins independently from the pelvic fins is only observed in some Stomiidae (Stomiiformes) and Pleuronectiformes. In stomiiform genera where this condition is observed, pectoral fins are present in larvae but are subsequently lost in juveniles and adults (Bolin 1939; Kawaguchi and Moser 1984; Fink 1985; Goodyear and Gibbs 1986; Hulley 1986; Kenaley and Hartel 2005). The loss of one or of both the pectoral fins also takes place during larval metamorphosis in Pleuronectiformes (Ahlstrom et al. 1984). This suggests that loss of the pectoral and pelvic fins are not entirely independent, which would be an expectation for a paired fins evolutionary module.

The dorsal fin is also responsible for a large part of the disparity in fin configuration in derived actinopterygians: there can be one, two or three separate dorsal fins, and it can also be entirely absent. There is usually a single anal fin, but it can also be lost, and there can occasionally be two anal fins. Similarly to the paired fins, there is evidence for non-independence in the dorsal/anal fin characters: orders with two anal fins also have two or three dorsal fins. Another source of disparity in median fin configurations is the adipose fin which is present in many derived actinopterygians. None of the euteleostan species that have an adipose fin have second (or third) dorsal fins: instead they generally have a single centrally placed dorsal fin and a posteriorly located anal fin (Reimchen and Temple 2004). Conversely, groups that are close relatives but lack an adipose fin tend to have a "fast-start" morphology with posteriorly placed dorsal and anal fins (Reimchen and Temple 2004; Temple and Reimchen 2008).

1.6.2 Evolutionary history of fish appendages

1.6.2.1 *Median fins*

Median fins are present even in the earliest vertebrates. The most basal agnathan fishes are equipped with fairly well-developed median fins which include, in most cases, a caudal fin, and elongated dorsal and ventral fins. For instance, the median ventral finfolds of myllokunmingiids span almost the full length of their bodies, as do their long sail-like dorsal fins (Shu et al. 1999; Hou et al. 2002; Shu et al. 2003a; Zhang and Hou 2004). Myxiniformes also often possess long median ventral finfolds, which although sometimes interrupted around the cloaca, are continuous with the caudal fin. These elongated median fins are reminiscent of the median larval finfold observed during the early ontogeny of more advanced fishes (van den Boogaart et al. 2012). They are also reminiscent of the extensive dorsal and ventral finfolds found in the more basal cephalochordates, which are continuous around the tail, but also around the anterior tip of the notochord (Andrews 1893; Kirkaldy 1895; Bigelow and Farfante 1948). The median fins of cephalochordates are described as being continuous with one of the two paired metapleural folds, but the latter can hardly be considered as fins because they are hollow structures filled with fluid (Rice 1880; Lankester 1889).

Even the most basal agnathans have a caudal fin. A caudal fin is absent, however, in *Gilpichthys greenei* and *Pipiscius zangerli*, two Carboniferous fossil fishes. Although these two taxa display clearly chordate characters, their assignment respectively to the Myxiniformes and Petromyzontiformes remains tentative and both have been interpreted as possible larval organisms (Bardack and Richardson 1977). Thus, the absence of a caudal fin could reflect a larval condition. It is also possible that the apparent lack of a caudal fin is merely a taphonomic artefact. This could arguably be the case for *Pipiscius* which presents a very posteriorly positioned dorsal fin that could certainly be interpreted as a dorsal extension of the caudal fin. Furthermore, only ten

specimens were used for the original description (Bardack and Richardson 1977). This explanation is however less likely for *Gilpichthys*, its original description being based on more than 100 specimens (Bardack and Richardson 1977).

In more advanced agnathans, a long-based preanal finfold is generally absent. Instead, many taxa possess a narrower-based and more posteriorly positioned anal fin. An anal fin is present in all anaspids that are sufficiently known from their postcranial anatomy. Furthermore, with the exception of two birkeniid anaspids for which a few spines and an anal plate located anteriorly to the anus (Kiaer 1924; Stetson 1928; Blom et al. 2002) were provisionally interpreted as evidence for a median ventral fin, a preanal finfold and an anal fin otherwise never co-occur in agnathans. Most modern hagfishes and lampreys lack an anal fin. However, the presence of a true anal fin has been observed in a few specimens of *Petromyzon marinus* (Vladykov 1973; Vladykov and Kott 1980) and of *Lampetra planeri* (Hume et al. 2014), a phenomenon that has been interpreted as a possible atavism (Janvier 2007, 2008). Anal fins have also been described in two Mississippian lampreys, *Hardistiella montanensis* (Janvier and Lund 1983) and *Mayomyzon pieckoensis* (Bardack and Zangerl 1968). Based on this evidence, Forey (1984) suggested that the absence of an anal fin could be a synapomorphy of recent lampreys. Additionally, the Carboniferous hagfish *Myxinikela siroka* is described as having dorsal and ventral fins (= anal fin?) that are continuous with the caudal fin, as in *Mayomyzon*, although in his original description, Bardack (1991) raised the possibility that *Myxinikela* might be a juvenile. *Myxinikela*, *Hardistiella* and *Mayomyzon* represent some of the oldest Myxiniformes and Petromyzontiformes for which complete non-larval specimens are known and, combined to the atavistic reappearance of an anal fin in *P. marinus* and *L. planeri*, this suggests that the appearance of an anal fin may have occurred before the anaspids. Thus, an anal fin could be a plesiomorphic characteristic of vertebrates, or even of craniates if the ventral fin of *Myxinikela* is homologous to an anal fin. An anal fin is absent in the oldest fossil lamprey, *Priscomyzon*, but phylogenetic analyses resolve *Mayomyzon* as the most basal

petromyzontid, while *Priscomyzon* is more derived (Gess et al. 2006; Morris and Caron 2014; McCoy et al. 2016). As for more crownward taxa, the presence of an anal fin is considered primitive for chondrichthyans, acanthodians and osteichthyans; its absence in some Paleozoic sharks (e.g., *Cladoselache*, stethacanthiids and symmoriids) is considered as a derived condition (Lund 1985).

As opposed to the median ventral fin, the long-based dorsal fins of myllokunmingiids are not so rapidly modified into narrow-based dorsal fins. Instead many agnathan taxa bear shorter-based and more posteriorly positioned dorsal fins (Petromyzontiformes, Loganelliiformes, Shieliiformes, Phlebolepidiformes, Furcacaudiformes, Osteostraci), while the Jamoytiiformes retain long-based dorsal fins. Long-based dorsal fins also occur in numerous chondrichthyan (e.g., *Pleuracanthus gaudryi*, *Chondrenchelys problematica*) and osteichthyan (e.g., *Regalescus glesne*, *Acanthurus major*) taxa. It is reasonable to assume that the dorsal fin is not constrained in its anterior extent and position, as opposed to the anal fin which cannot extend anteriorly past the position of the anus. The Gymnotiformes provide a striking example: these fishes have elongated anal fins that extend along the majority of the ventral midline of the body, yet the anus is displaced anteriorly in these forms and is positioned under the pectoral fins or even under the head, thus remaining in front of the anterior limit of the anal fin (Gayet et al. 1994; Albert 2001; Albert and Crampton 2009).

1.6.2.2 *Duplications of the dorsal fins*

Duplications of the dorsal fin seem to have occurred numerous times independently during the evolutionary history of fishes. Most extant lampreys have two dorsal fins. Among osteostracans, *Ateleaspis*, *Aceraspis* and *Hirella* possess two dorsal fins and are resolved as basal members of this group (Janvier 1981b, a, 1985a; Sansom 2009; Scott and Wilson 2012). Among the most basal orders of placoderms, antiarchs and stensioellids possess a single dorsal fin, but the material for brindabellaspids and

pseudopetalichthyids precludes interpretation of dorsal fin characters. Among acanthodians, climatiiforms, diplacanthiforms and ischnacanthiforms have two dorsal fins. Acanthodiforms possess a single dorsal fin but this is considered as secondarily derived for this group.

Lund (1985) expressed that the plesiomorphic condition for the number of dorsal fins in chondrichthyans could not be determined at the time and could just as well have been a single dorsal fin or two dorsal fins. The most basal articulated undisputed elasmobranchs known from the fossil record, *Doliodus problematicus* and *Antarctilamna prisca*, have anterior dorsal fins, but most of the postcranial region is unknown and thus insufficient to assess the presence of a posterior dorsal fin (Young 1982; Miller et al. 2003). Additionally, in the *Antarctilamna* material, a spine with a shallow insertion that had initially been interpreted as a displaced dorsal fin spine is now thought to be a pectoral fin spine, whereas a second type of spine with a deeper insertion is interpreted as a median fin (Miller et al. 2003; Wilson et al. 2007; Hanke and Wilson 2010). Furthermore, phylogenies have not reached a stable consensus concerning the interrelationships of basal Euchondrocephali (e.g., Lund and Grogan 1997; Grogan and Lund 2008; Lund et al. 2014). Our supertree analysis places the iniopterygians as the most basal euchondrocephalan order, although they are resolved as the sister clade to all other chondrichthyans in Lund et al. (2014). Of course, in light of the growing support for the hypothesis that acanthodians are stem chondrichthyans, this would imply that the plesiomorphic condition for the total group chondrichthyans is in fact the presence of two dorsal fins.

Among osteichthyans, the presence of two dorsal fins has been considered as plesiomorphic (Schultze 1986). *Guiyu oneiros*, resolved as a stem sarcopterygian (Qiao et al. 2016), was originally reconstructed with a single dorsal fin (Zhu et al. 2009), but has recently been reinterpreted as having two dorsal fins (Zhu et al. 2012a). All other sarcopterygians have two dorsal fins, with the exception of a few dipnoans,

elpistostegalians and tetrapods. The Early Devonian *Dialipina* is resolved either as a basal osteichthyan (Friedman 2007; Brazeau 2009; Davis et al. 2012; Dupret et al. 2014; Brazeau and de Winter 2015; Giles et al. 2015c; Burrow et al. 2016; Lu et al. 2016a), or as the most basal actinopterygian (Taverne 1997; Schultze and Cumbaa 2001; Zhu and Schultze 2001; Zhu et al. 2006; Zhu et al. 2009; Giles et al. 2015b; Long et al. 2015), and possesses two dorsal fins (Schultze and Cumbaa 2001). Among other non-acanthomorph actinopterygians, a second dorsal fin is also found in a single fossil Ionoscopiformes genera (Brito 2000), and in a few extant Siluriformes belonging to the Plotosidae (Jayaram 1981, 1982; Ferraris 1999; Nelson et al. 2016). This suggests that the presence of two dorsal fins would have been lost early during actinopterygian evolution (Cloutier and Arratia 2004), but that this character would have subsequently been reacquired more than once independently.

The dorsal fin(s) of acanthomorphs can be interpreted in two different ways. Acanthomorphs are characterized by the possession of a spinous dorsal fin (Johnson and Patterson 1993). In some taxa the spinous and soft dorsal fins are continuous and connected by a fin web, whereas in others they are widely separated. One hypothesis is that the anterior spinous dorsal fin found in acanthopterygians results from a duplication of the posterior soft dorsal fin module (Mabee et al. 2002). We favored this hypothesis and have considered that dorsal fins where the bases were not connected by the fin web constituted separate dorsal fins. Another hypothesis is that the second or third dorsal fins in acanthopterygians results from the subdivision of an originally more elongated fin (Sandon 1956). As such, acanthomorphs retain a single dorsal fin which is regionalized, thus giving the impression that there are two (or three) dorsal fins (Janvier 1996b). Our supertree analysis places the Lampridiformes at the base of the acanthomorph radiation. The Aipichthyiodea, resolved as stem Lampridiformes (Davesne et al. 2014; Delbarre et al. 2015), possess a single dorsal fin, for which the anterior portion is generally supported by two to five fin spines (Otero and Gayet 1996; Otero 1997; Murray and Wilson 2014; Delbarre et al. 2015), although there are 12 fin

spines in *Homalopagus multispinosus* (Murray and Wilson 2014). In crown Lampridiformes, dorsal fin spines are present in Veliferidae but are considered to have been secondarily lost in other forms (Davesne et al. 2014). In light of this evidence, the hypothesis of a regionalized dorsal fin cannot be ignored.

Taken together, the phylogenetic distribution of dorsal fin conditions suggests that duplications of the dorsal fin occurred multiple times during the evolutionary history of fishes. It also suggests that two dorsal fins might have been the condition for the common ancestor to both osteostracans and gnathostomes. This character would have subsequently been lost and then occasionally reacquired in many fish lineages.

1.6.2.3 *Paired fins*

The first evidence of true paired fins in craniates is in the Anaspidiformes and Jamoytiiformes, generally in the form of long ribbon-like paired folds that are ventrolateral in position. A notable exception can be found in the Myxiniformes, where for a single genera, *Neomyxine*, we tentatively scored for the presence of ventrolateral paired fins. *Neomyxine* possesses paired folds of skin located immediately above the gill openings (Richardson 1953, 1958; Zintzen et al. 2015). These skin folds are not used for swimming but rather as support when specimens settle on the substrate (Richardson 1958). Furthermore, because these structures are located dorsally to the branchial apertures and because *Neomyxine* is not basal relative to other hagfishes, these paired skin folds are unlikely to be homologous to the ventrolateral paired fins found in other agnathans (Janvier 1978; Donoghue et al. 2000). Thus, excluding *Neomyxine*, ventrolateral paired fins appear with the anaspids and can also be found in some thelodonts. The question regarding the homology of these paired fins has been debated for many years. Some authors consider that true paired fins must be constricted and supported by an endoskeletal girdle and fin radials (Janvier 1996a; Johanson 2010).

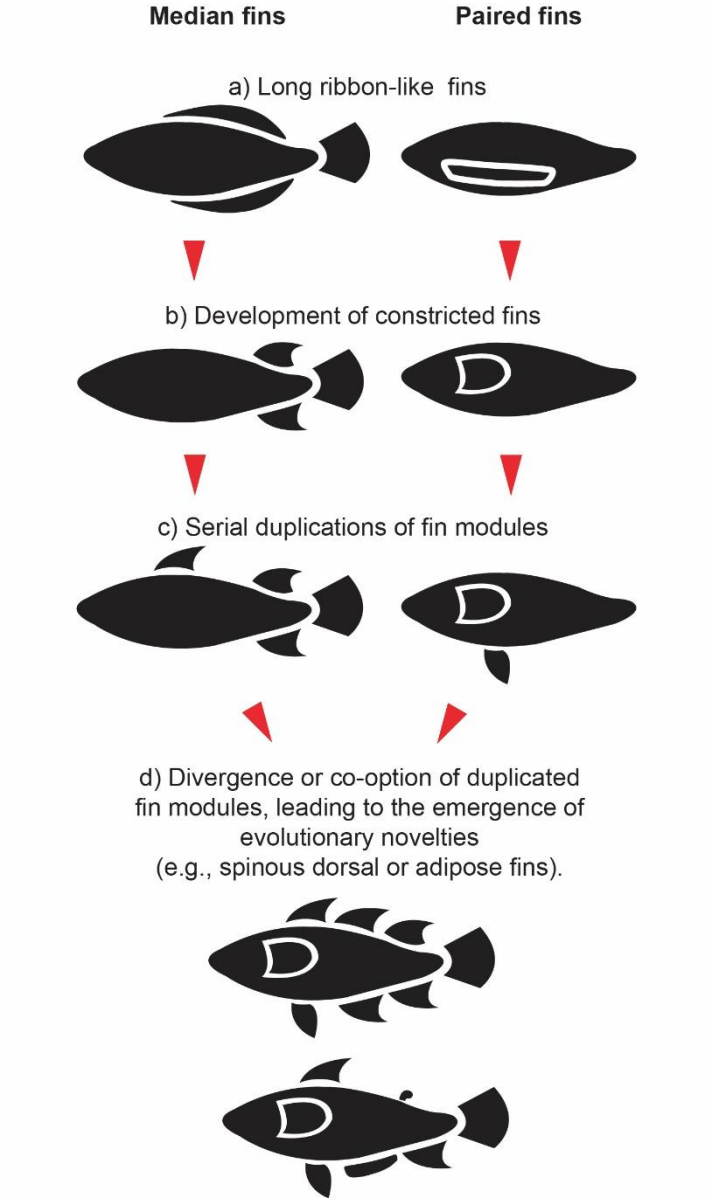

Figure 8: Hypothesized scenario for the evolution of median and paired fins. Both median and paired fins developed first as elongated ribbon-like structures (A) that are gradually modified into narrow-based fins (B). Serial duplications of fin modules lead to the emergence of novel fins such as the pelvic fins or a second dorsal fin (C). Divergence or co-option of some fin modules also leads to the evolution of novel fins, such as the adipose fin of euteleosts or the spinous dorsal fin of acanthomorphs (D).

An alternative hypothesis is that paired fins evolved first as lateral extensions of the body, and that paired girdles only appeared later during the evolutionary history of basal vertebrates (Zug 1979). Shubin et al. (1997) proposed an evolutionary scenario whereby (1) paired fins first appeared as elongated ventrolateral expansions along the body wall, (2) these expansions were replaced first by pectoral appendages only, (3) and later pectoral and pelvic fins appeared as serial homologues among gnathostomes. We find the latter hypothesis reasonable: it would not be surprising that paired and unpaired fins share a similar evolutionary history (Figure 8) considering the remarkable anatomical and developmental similarities between the paired and unpaired fins (Goodrich 1906; Bemis and Grande 1999; Freitas et al. 2006). Furthermore, based on gene expression patterns during fin development in lampreys and sharks, it has been suggested that the genetic programming associated with median fin development was subsequently redeployed to the lateral mesodermal plate, giving rise to the paired fins (Freitas et al. 2006; Freitas et al. 2014). A previous study focusing on gene expression patterns in cephalochordates had similarly led Schubert et al. (2000) to hypothesize that part of the developmental programs involved in tail outgrowth in basal chordates could have been co-opted towards paired appendage development in vertebrates. Alternatively, it could be argued that paired fins evolved multiple times independently during the evolutionary history of vertebrates (Denison 1951).

As for narrow-based paired fins, true pectoral fins are considered to have appeared with the osteostracans, although pituriaspids also have pectoral fenestrae suggesting that pectoral fins were present in these taxa as well (Young 1991). Furthermore, some thelodonts possess paired fins that are in a pectoral position (Coates 2003; Märss et al. 2007; Wilson and Märss 2012). The pectoral fins of osteostracans are supported by endoskeletal elements and are under muscular control: they can thus be considered as homologous to the pectoral fins of gnathostomes (Forey and Janvier 1993; Coates 2003; Sansom 2009). Girdle-supported pelvic fins are absent in agnathans (Janvier 1978; Johanson 2010; Zhu et al. 2012a; Zhu et al. 2012b), and are first observed among

placoderms (Janvier 1996b; Zhu et al. 2012b; Sansom et al. 2013). Antiarch placoderms have been resolved at the base of the gnathostome diversification in most of the recent phylogenetic studies (Brazeau 2009; Davis et al. 2012; Zhu et al. 2013; Dupret et al. 2014; Long et al. 2015; Burrow et al. 2016) and were thought to be devoid of pelvic fins (Young 2010). However, Zhu et al. (2012b) recently described a pelvic girdle in *Parayunnanolepis*. Additionally, our supertree analysis places the Pseudopetalichthyida stemward to the antiarch placoderms, making it the most basal gnathostome order. The most well-preserved pseudopetalichthyid articulated material belongs to *Pseudopetalichthys problematica*, which is known to possess both pectoral and pelvic fins. This suggests that the presence of pelvic fins is likely to be plesiomorphic for gnathostomes.

1.6.3 Evidence for fin evolutionary modules

Based on the mapping of fin characters on the supertree, some pairs of fins are more frequently associated, either through coordinated duplication events or through coordinated losses, which is congruent with hypotheses that together they form evolutionary modules. This is the case for the dorsal and anal fins where the presence of a second anal fin is associated with the presence of a second or third dorsal fin. Mabee et al. (2002) suggested that the dorsal and anal fins were linked through the presence of both positioning and patterning modules. Although patterning modules refer to the development of endo- and exoskeletal supports (Mabee et al. 2002; Cloutier 2010; Grünbaum et al. 2012), the effect of the patterning module could extend to the resorption of the larval median finfold. As such, the mechanism underlying duplication of a non-resorption zone of the larval finfold could very well be reflected dorso-ventrally. This pattern also emerges in their coordinated loss or duplication patterns. For instance, in actinopterygians, results from the multiple correspondence analyses suggest that loss of the dorsal, anal and caudal fins can be coordinated, and also that the presence of a second anal fin co-occurs with the presence of a third dorsal fin.

Likewise, the results also show that loss of the pectoral and pelvic fins can be coordinated. Coordination of fin losses is not limited to actinopterygians: the results of the multiple correspondence analyses for chondrichthyans and sarcopterygians also show coordinated losses of the median fins. Evidence for a dorsal and anal fins evolutionary module has been proposed for lungfish, in light of the observations that in earlier forms, the dorsal and anal fins present equivalent positions along the antero-posterior body axis, that they have similar morphologies, particularly with respect to fin supports, and that they were coordinately lost at the end of the Devonian (Johanson et al. 2009). It is unclear however if the dorsal and anal fins module suggested in Johanson et al. (2009) involves the anterior dorsal fin, the posterior dorsal fin, or both dorsal fins. At a population scale, it was found that in the Arctic char (*Salvelinus alpinus*), anatomical and developmental patterning of the dorsal and anal fins were highly similar, but differed largely from that of the caudal fin: this was interpreted as supporting the patterning modules proposed by Mabee et al. (2002) for the dorsal and anal fins (Cloutier et al. 2010; Grünbaum et al. 2012). Additionally, a patterning module was also hypothesized for the caudal fin (Grünbaum et al. 2012). Contrastingly, in a recent study focusing on variational modularity in two cyprinid species, we showed good support for the hypothesis that the dorsal, anal and caudal fins formed one variational module including the tail, while the paired fins formed another variational module (Larouche et al. 2015). Because modularity is a hierarchical concept, a hypothesis of evolutionary modularity worth investigating is that the median fin system as a whole could constitute one module, the paired fin system could constitute a second independent module, and the dorsal and anal fins could constitute a third module nested within the median fins module (Figure 9). Quasi-independent median and paired fin modules would help explain why there is so much disparity in median fin configuration in chondrichthyans, compared to the paired fins that are largely unaffected.

We have demonstrated that the co-occurrence of some sets of fins is non-random. Among these, the pectoral, pelvic, dorsal, anal and caudal fins have all been found to

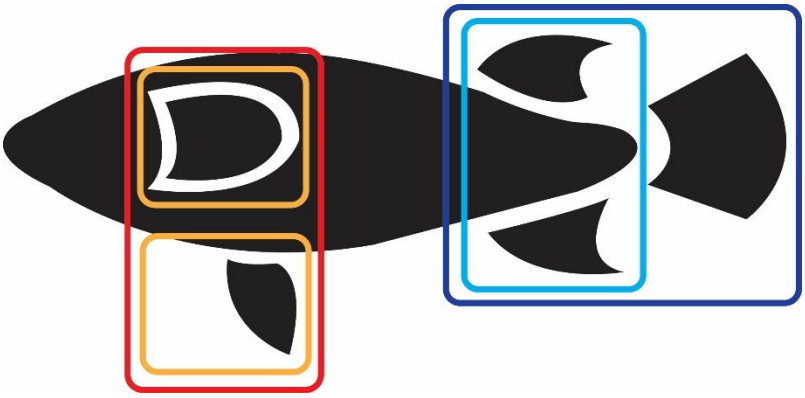

Figure 9: Hypothesized fin modules. The pectoral and pelvic fins form a paired fins evolutionary module that can be dissociated, leading to individualized pectoral and pelvic fin modules. The dorsal and anal fins form a second evolutionary fin module nested within a larger median fins evolutionary module.

be non-independent. This reflects the most common fin combinations found in the dataset where all of these fins co-occur, more specifically the fin combinations that are characteristic of most actinopterygian orders (single dorsal and anal fins, a caudal fin, pectoral and pelvic fins), and of most chondrichthyan and sarcopterygian orders (two dorsal fins, a single anal fin, a caudal fin, pectoral and pelvic fins). When the analysis focuses on unique fin combinations, only the pectoral/pelvic fins show non-independence. The strong relationship between the pectoral and pelvic fins is concurrent with hypotheses that they form a paired fins evolutionary module.

A relationship was also found between the adipose fin and the median ventral fin. The adipose fin is considered as an evolutionary novelty among teleostean taxa and might also constitute a new fin module (Maisey 2009; Stewart and Hale 2013). An adipose fin evolved at least twice independently, once within the Otophysi and a second time in the Euteleostei (Stewart and Hale 2013; Stewart et al. 2014). Development of the adipose fin is known to differ between otophysans and euteleosteans, supporting the hypothesis of multiple independent origins: in Characiformes, the adipose fin appears

as an outgrowth following the complete resorption of the larval finfold, while in Salmoniformes, it develops as a remnant of the larval finfold (Stewart et al. 2014). As for the median ventral fin, the positive relationship with the adipose fin stems from a few euteleostean families that, in addition to the adipose fin, possess a rayless finfold in front of the anal fin that is often described as a ventral adipose fin (Retropinnidae, Stomiidae, Paralepididae). However, a similar ventral fin is also found in at least one family, the Sundasalangidae (Clupeiformes), prior to the appearance of the adipose fin, as well as in eutelesostean families that do not have adipose fins (Phallostethidae, Hypoptychidae). As opposed to the adipose fin which has been the object of numerous recent investigations (Reimchen and Temple 2004; Temple and Reimchen 2008; Stewart and Hale 2013; Stewart et al. 2014; Stewart 2015), to our knowledge no work has focused on the origin or homology of the so-called ventral adipose fin. Developmental and histological work would be necessary to establish if this median ventral fin is homologous among these taxa.

A dorsal-anal fin module is well supported by developmental data (Crotwell et al. 2001; Crotwell et al. 2004; Freitas et al. 2006; Cloutier 2010; Cloutier et al. 2010; Grünbaum et al. 2012). It has also been inferred based on the similarities in the relative positioning of these two fins across species (Mabee et al. 2002). Because the positioning module inferred by Mabee et al. (2002) has been identified at a macroevolutionary scale, it qualifies as an evolutionary module. Herein, we provide further evidence for a dorsal-anal fin evolutionary module, with indications that its effect also extends to the coordinated losses and duplications of these fins in different species.

Co-occurrence of the pectoral and pelvic fins is extremely well supported in our analyses. Both paleontological and embryological studies support the idea that the pelvic fins could have originated by a duplication of the pectoral fins module (Coates 1993, 1994; Ruvinsky and Gibson-Brown 2000; Tanaka and Onimaru 2012). From this point of view, it follows that the co-occurrence of these two fins would be expected.

An alternative possibility is that the pectoral and pelvic fin modules have dissociated and become independent modules during the evolutionary history of fishes (Coates 1994; Coates and Cohn 1998; Coates et al. 2002; Hanke and Wilson 2006; Hall 2010). As evidence for this latter hypothesis, Coates and Cohn (1998) mentioned that there is no example in which the pelvic appendages are a direct copy or identical serial homologues of the pectoral fins. One could argue however that the paired fins present extremely similar morphologies in chimaerids (Riley et al. 2017), and in many sarcopterygians (Schultze 1986; Zhu et al. 2012a). Furthermore, biserial fin designs evolved convergently in pectoral and pelvic fins in some chondrichthyan and sarcopterygian taxa, as did uniserial fin designs in osteolepiforms (Shubin 2002). Considering that independent loss of the pectoral or pelvic fins occurs almost only in actinopterygians, perhaps the dissociation of the paired fins module is a generalized characteristic for this group, which was independently acquired in eugeneodontiform sharks.

1.7 Conclusions

Although the sequential emergence of fins among fishes has been discussed on empirical grounds, the results from this analysis support a longstanding idea that both the median and paired fins would have appeared first as long-based or ribbon-like structures, before being modified into more constricted appendages. Additionally, for the first time, we have a quantified picture of the covariation in fin presence at a large phylogenetic scale. Our results highlight that even with a dataset comprising semi-quantitative characters, there is compelling evidence that the pectoral and pelvic fins, and the dorsal and anal fins form two distinct evolutionary modules. The results also suggest an interesting hypothesis whereby the dorsal/anal fins module could be nested within a larger median fins module. Combined with the results from our analysis on variational modularity in cyprinids (Larouche et al. 2015), this suggests that patterns of morphological integration and modularity that are identified within populations can

translate into integration at a macroevolutionary scale. An important next step will be to validate this hypothesis using fully quantitative methods, as well as to investigate the consequences of these putative evolutionary modules on patterns of morphological disparity. Because the hypotheses of modularity that we are testing are largely based on evidence from developmental data, this would provide a striking example linking developmental to variational and evolutionary modules.

CHAPITRE II

TÊTE, CORPS ET NAGEOIRES : PATRONS D'INTÉGRATION MORPHOLOGIQUE ET DE MODULARITÉ CHEZ LES POISSONS

2.1 Résumé

Les actinoptérygiens présentent une importante disparité morphologique, particulièrement en termes de variations dans la position, la taille et la forme de leurs nageoires. L'une des hypothèses qui pourrait expliquer l'accumulation de disparité dans la morphologie des nageoires est que celle-ci est facilitée par une organisation modulaire. Selon cette hypothèse, des modules de nageoires agiraient comme des unités quasi-indépendantes au cours de l'ontogénie ou de l'évolution, facilitant leur évolvabilité. Nous avons analysé la modularité variationnelle des nageoires chez deux espèces de Cyprinidae, le poisson zèbre (*Danio rerio*) et le ventre rouge du Nord (*Chrosomus eos*), afin de déterminer quels sous-ensembles de nageoires sont quasi-indépendants et le plus fortement intégrés dans leur positionnement. Une série d'hypothèses de modularité ont été évaluées en utilisant une combinaison de méthodes faisant appel aux outils de la morphométrie géométrique. L'hypothèse voulant que les nageoires dorsale et anale appartiennent à un module variationnel incorporant l'ensemble du tronc postérieur et de la queue est fortement supportée, ce qui peut s'expliquer par le fait que ces deux espèces utilisent un mode de locomotion subcaranguiforme. Les hypothèses voulant que les nageoires paires et la tête forment chacun des modules variationnels sont aussi supportées, quoique moins fortement. Le support pour des modules variationnels de nageoires est moindre que ce qui était attendu considérant la panoplie d'observations développementales qui supportent la modularité des nageoires. Ceci pourrait résulter d'une dissociation des modules de positionnement des nageoires au cours de l'évolution des actinoptérygiens, un processus qui a déjà été suggéré pour les nageoires dorsale et anale. Il est aussi possible

que les modules de nageoires inférés à partir de données développementales ne se traduisent pas directement en modules variationnels : les modules variationnels peuvent incorporer les signaux de plusieurs processus développementaux qui se superposent partiellement au cours de l'ontogénie. Ainsi, une correspondance de un pour un entre les modules développementaux et variationnels ne devrait pas toujours être attendue.

Cet article, intitulé *Head, Body and Fins: Patterns of Morphological Integration and Modularity in Fishes*, a été corédigé par moi-même ainsi que par Richard Cloutier et Miriam L. Zelditch. Cet article a été publié dans le journal international *Evolutionary Biology* en septembre 2015. Le projet a été élaboré par Richard Cloutier et par moi-même. Les aspects méthodologiques de l'analyse des données ont été développés par Miriam L. Zelditch et par moi-même. En tant que premier auteur, mes contributions incluent notamment la revue de la littérature pertinente, la préparation et la prise de photos des spécimens, la digitalisation des landmarks, la complétion des analyses et la production des figures et du matériel supplémentaire. J'ai rédigé la première version du manuscrit, et tous les auteurs ont contribué aux versions subséquentes jusqu'à la production de la version finale. Une partie des résultats a été présentée dans un congrès international, soit lors du *Evolution 2014 Annual Meeting* en juin 2014 à Raleigh (Caroline du Nord). Une partie de ces résultats ont aussi été présentés sur invitation du Dr. Brian K. Hall dans le cadre d'un *Mini-Symposium on Fish Evo-Devo* qui s'est déroulé au Mount St-Vincent University, à Halifax (Nouvelle-Écosse), en février 2015.

Je tiens à remercier V. E. Roy pour son assistance dans la commande de spécimens de poissons zèbres et pour son aide dans l'entretien des aquariums. Je remercie aussi D. Potvin-Leduc et O. Cloutier pour des suggestions artistiques quant à la conception graphique de certaines des figures. Ce projet a été supporté financièrement en partie par le Conseil de Recherches en Sciences naturelles et en Génie du Canada (BESC-M

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Head, Body and Fins: Patterns of Morphological Integration and Modularity in Fishes

2.2 Abstract

Actinopterygians demonstrate high levels of morphological disparity, especially in the variation of fin positions, sizes and shapes. One hypothesis to explain the diversity of fin morphologies is that it is facilitated by a modular organization. According to this hypothesis, fin modules would be quasi-independent during ontogeny or evolution, facilitating their evolvability. We investigated variational modularity of fins in two cyprinid species, the zebrafish (*Danio rerio*) and the Northern redbelly dace (*Chrosomus eos*), to determine which subsets of fins are quasi-independent and which are most highly integrated in positioning. Hypotheses of modularity were evaluated using a combination of methods suitable for analyses of landmarks. The hypothesis that the dorsal and anal fins belong to a posterior trunk and tail module is strongly supported, a finding that can be explained by the use of subcaranguiform locomotion in these two species. There is also some support for the hypothesis that the paired fins and head region each constitute variational modules. The support for fin variational modules is weaker than expected considering the wealth of developmental evidence supporting fin modularity. This might be related to a dissociation of the fin positioning modules during actinopterygian evolution, a process that had already been suggested for the dorsal and anal fins. Alternatively, the fin modules inferred from developmental data might not directly translate into variational modules: variational modules can incorporate the signals from numerous partially overlapping developmental processes so that one to one correspondence between developmental and variational modules is not always expected.

KEYWORDS: ray finned fishes, fin positioning, variational modules, functional integration, geometric morphometrics.

2.3 Introduction

Among fishes, actinopterygians have achieved a remarkable ecological and evolutionary success (Lauder and Liem 1983), resulting in over 30 000 living species as well as an abundant fossil record (Nelson 2006). No less impressive is the extent of morphological disparity that can be observed among them, notably in terms of fin configurations that refers to relative positioning, sizes and shapes. Indeed, many changes in modes of feeding and locomotion are associated with changes in structure, size, number and position of fins (Webb 1982; Lauder and Liem 1983; Webb 1984; Lauder and Drucker 2004; Shubin and Davis 2004). A property of living systems that is well suited to explain the origin of morphological disparity is their modular organization (Wagner 1996; Hansen 2003; Wagner et al. 2007; Pavlicev and Hansen 2011).

Organisms are hypothesized to be constructed from distinct sub-units termed modules that are highly integrated internally and behave quasi-independently during ontogeny and evolution (Wagner 1996; von Dassow and Munro 1999; Hansen et al. 2003; Klingenberg et al. 2003; Wagner et al. 2007; Kuratani 2009). Modularity is tightly linked to the concept of morphological integration, which postulates that functionally or developmentally related traits should form highly cohesive morphological units (Olson and Miller 1958; Cheverud 1982; Zelditch 1987; Cheverud 1996a; Chernoff and Magwene 1999). In this context, modularity refers to the difference in levels of integration of traits within modules relative to those between neighboring modules, with the expectation that modules will display comparatively high levels of morphological integration and form quasi-autonomous units (Wagner 1996; Magwene 2001; Klingenberg 2008, 2009). Modularity is considered as an important aspect for the evolvability of living systems (Bonner 1988; Raff 1996; Wagner 1996; Wagner and Altenberg 1996) because individual modules can be improved upon without interfering

with other subunits that have already been optimized (Wagner 1996; Wagner and Altenberg 1996; Hansen 2003; Hansen et al. 2003). In this sense, modular fins could help explain the extent of morphological disparity in fin configurations observed among fishes.

Modules can be categorized according to the types of processes in which they are involved. Developmental modules are quasi-autonomous with respect to their patterns of formation and differentiation (Raff 1996; Wagner and Mezey 2004; Wagner et al. 2007). They are often identified based on the criteria that they should be developmentally autonomous parts of an organism, meaning that they can complete their development even if placed outside their normal anatomical location (Raff 1996; Bolker 2000; Wagner and Mezey 2004; Wagner et al. 2007). Variational modules refer to sets of phenotypic traits that are strongly integrated in their variation and semi-independent of other sets due to the underlying patterns of expression of pleiotropic genes (Wagner and Altenberg 1996; Wagner and Mezey 2004; Wagner et al. 2007). One way to recognize variational modules is to study correlations between quantitative characters (Olson and Miller 1958; Cheverud 1982; Wagner 1996). Variational modules can differ from developmental modules because one or more of the latter can combine to form a single variational module (Wagner and Mezey 2004). Variational modules can also become independent units of evolutionary change, making them evolutionary modules as well (Wagner 1996; Schlosser and Wagner 2004; Wagner and Mezey 2004; Klingenberg 2008).

A number of modules have been proposed for fins in fishes. One hypothesis is that the dorsal and anal fins originally shared a so-called positioning module (Mabee et al. 2002), based on the observation that basal actinopterygians tend to have symmetrically positioned dorsal and anal fins relative to the antero-posterior body axis. This median fins positioning module is thought to have been initially coupled to a putative patterning module controlling differentiation patterns of skeletal support elements in

the dorsal and anal fins (Mabee et al. 2002). Lending support to this hypothesis, in the zebrafish, it was found that the dynamic expression patterns of the genes involved during fin formation (e.g., *Gdf5*, *bmp2a*, *bmp2b*) are similar for both the dorsal and anal fins and are associated with the bidirectional radial development patterns observed in both of these fins (Crotwell et al. 2001; Crotwell et al. 2004). The integrated development of the endo- and exoskeletal components of the median fins is also thought to be regulated by a developmental module (Mabee et al. 2002). Another proposed median fin module is that of the acanthopterygian first dorsal fin, which is thought to have resulted from a duplication of the posterior dorsal fin module followed by divergence, whereby finrays have been replaced by spines (Mabee et al. 2002; Stewart et al. 2014). As for the paired fins, one hypothesis based on embryological and paleontological evidence, is that pelvic fins originated from a duplication of the pectoral fins module (Coates 1993, 1994; Ruvinsky and Gibson-Brown 2000; Tanaka and Onimaru 2012). However, the independent losses and modifications of the pelvic fins relative to the pectoral fins suggest that both became individuated as modules during the evolution of fishes (Coates 1994; Coates et al. 2002; Hall 2010).

The fin modules hypothesized by Mabee et al. (2002), described as patterning and positioning modules, do not correspond to the types of modules usually considered by developmental or evolutionary theories. Although inferred from developmental sequences of fin skeletal supports, the patterning modules mentioned above do not strictly conform to the definition of developmental modules, nor to the evolutionary modules that are thought to enhance evolvability. Instead, they are based on similarities in developmental sequences of the skeletal support structures and in this sense, might be interpreted as variational modules. As for the positioning modules proposed for the median fins, these are based on comparisons among species (Mabee et al. 2002), so that they might be considered evolutionary modules. However, it is not clear whether they are also variational modules, because those modules need to be identified through patterns of variation. Thus, in this paper, we investigate variational modularity of fin

positioning in two actinopterygian species: the zebrafish (*Danio rerio*) and the Northern redbelly dace (*Chrosomus eos*). Furthermore, we examine both the median fin positioning modules proposed by Mabee et al. (2002) and positional modularity of the paired fins. One of our expectations was that the dorsal and anal fins would form a variational module based on the accumulated evidence for similarities in their development and relative positioning. We also expected the pectoral and pelvic fins to form a variational module, based on the hypothesis that the pelvic fins originated from a duplication of the pectoral fins module.

2.4 Methods

2.4.1 Sample

Morphological integration and hypotheses of modularity were examined using two species of Cyprinidae: the zebrafish (*D. rerio*) and the Northern redbelly dace (*C. eos*). Zebrafish rarely exceed 40 mm in standard length and are widely distributed in the Indian subcontinent where they are known to inhabit streams, canals, ditches, ponds and slow-moving or even stagnant bodies of water (McClure et al. 2006; Engeszer et al. 2007). Northern redbelly dace can reach lengths of 70 to 80 mm (Phillips 1969) and are generally found in North-American boggy lakes, streams and ponds (Scott and Crossman 1973). The two species are not closely related within the Cyprinidae, each one belonging to a separate sub-family (*C. eos*, Leuciscinae; *D. rerio*, Rasborinae) (He et al. 2008).

Zebrafish specimens were acquired from a supplier for the aquarium trade (Mirdo Importations Canada Inc.), and euthanized using MS222 (CAS 886-86-2). Northern redbelly dace specimens were collected with bait traps in Lunettes Lake, Rimouski (QC, Canada). Handling of animals complied with the guidelines of the Canadian Council of Animal Care. All fishes were fixed in 4% neutrally buffered formalin, and

preserved in 70% alcohol. A sample of 108 specimens was used for each species. Fishes were photographed on their left side using a Nikon D300 digital camera. The camera was mounted on a copy stand to control for problems of parallax and to standardize the distance from the object.

2.4.2 Geometric Morphometrics

To analyze fin-positioning, we placed nine landmarks at the fin insertion points and five others were placed at the anterior limit of the rostrum, anterior and posterior limits of the eye and antero-dorsal and antero-ventral limits of the gill cover (Figure 10, Table 7). A series of 55 semi-landmarks were used to provide information about curvature where landmarks could not be consistently positioned. Because spacing between semi-landmarks is arbitrary, they contain less information than landmarks but are nonetheless useful when the latter cannot fully capture the information about shape. Semi-landmarks were placed along the posterior margin of the gill cover, the base of each fin and the tail region, which we consider to be the posterior part of the body extending behind dorsal and anal fins and supporting the caudal fin.

Digitized coordinates were superimposed using a General Procrustes Analysis (Rohlf and Slice 1990). Semi-landmarks require an additional step to remove the variation

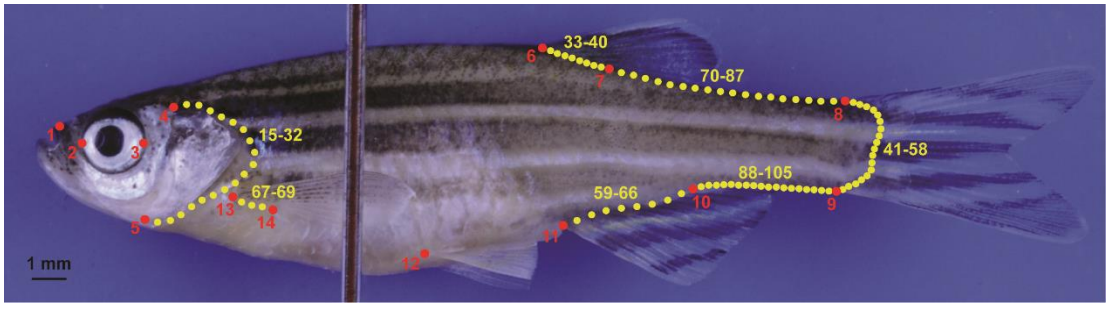

Figure 10: Zebrafish (*Danio rerio*) specimen showing landmark (red) and semi-landmark (yellow) positioning scheme. See Table 1 for description of landmark positions.

Table 7 : Description of landmarks for the analyses of geometric morphometry.

No	Description of landmarks
1	Anterior limit of the rostrum
2	Anterior limit of the eye
3	Posterior limit of the eye
4	Antero-dorsal limit of the gill cover
5	Antero-ventral limit of the gill cover
6	Anterior insertion of the dorsal fin
7	Posterior insertion of the dorsal fin
8	Dorsal insertion of the caudal fin
9	Ventral insertion of the caudal fin
10	Posterior insertion of anal fin
11	Anterior insertion of the anal fin
12	Insertion of the pelvic fin
13	Dorsal insertion of the pectoral fin
14	Ventral insertion of the pectoral fin

owing to their arbitrary position along the curve. Two criteria were used for the optimal semi-landmark superimposition: (1) the minimum bending energy of the deformation between the target shape and the reference (mean) shape (Green 1996; Bookstein 1997), and (2) the minimum chord (Procrustes) distance between these two shapes (Sampson et al. 1996).

2.4.3 Standardizing for Preservational Artifacts and for Size

Fish body shape is often distorted during fixation and preservation, resulting in a dorsal bending along the body axis that can substantially contribute to the variation within a sample. We used principal component analyses (PCA) to visualize the major sources of variation. We found that this bending explained 37% of the variation for *C. eos* and

25% for *D. rerio*. The bending effect was removed using a feature in tpsUtil (Rohlf 2013a) whereby a series of landmarks are identified that should be perfectly aligned, then a quadratic function derived from this baseline is applied to the entire landmark configuration to straighten each specimen individually.

For both species, the samples are likely heterogeneous in terms of the age of the specimens they contained. Because shape variation might be integrated due to age variation (ontogenetic allometry), obscuring evidence for modularity, we tested for the covariance between shape and size. A small yet significant effect of size was found for both species (*D. rerio*: variance explained = 4%, $p < 0.002$; *C. eos*: variance explained = 9%, $p < 0.001$). Variation in shape correlated with size was thus statistically removed from the shape data.

2.4.4 Testing Hypotheses of Modularity

2.4.4.1 A priori *hypotheses*

The 19 *a priori* hypotheses are represented in Figure 11. These hypotheses are based on fin modules suggested in the literature (Coates 1993, 1994; Mabee et al. 2002; Hall 2010; Grünbaum et al. 2012), as well as on functional and topological relationships among structures. Various combinations of the presence or absence of each of the putative modules were tested, resulting in a total of 19 *a priori* hypotheses (Table 8, Figure 11). To fit these models, we used three approaches: (1) a distance-matrix method, which calculates correlations between shapes of subsets of landmarks, yielding a correlation matrix that can be used to test hypotheses of modularity, (2) a minimum-deviance method, which assesses the goodness-of-fit of the covariance matrix derived from a model to the data, and (3) a measure of the strength of the association between subsets of landmarks, Escoufier's RV coefficient, which is then compared to the distribution obtained by randomly partitioned subsets of coordinates.

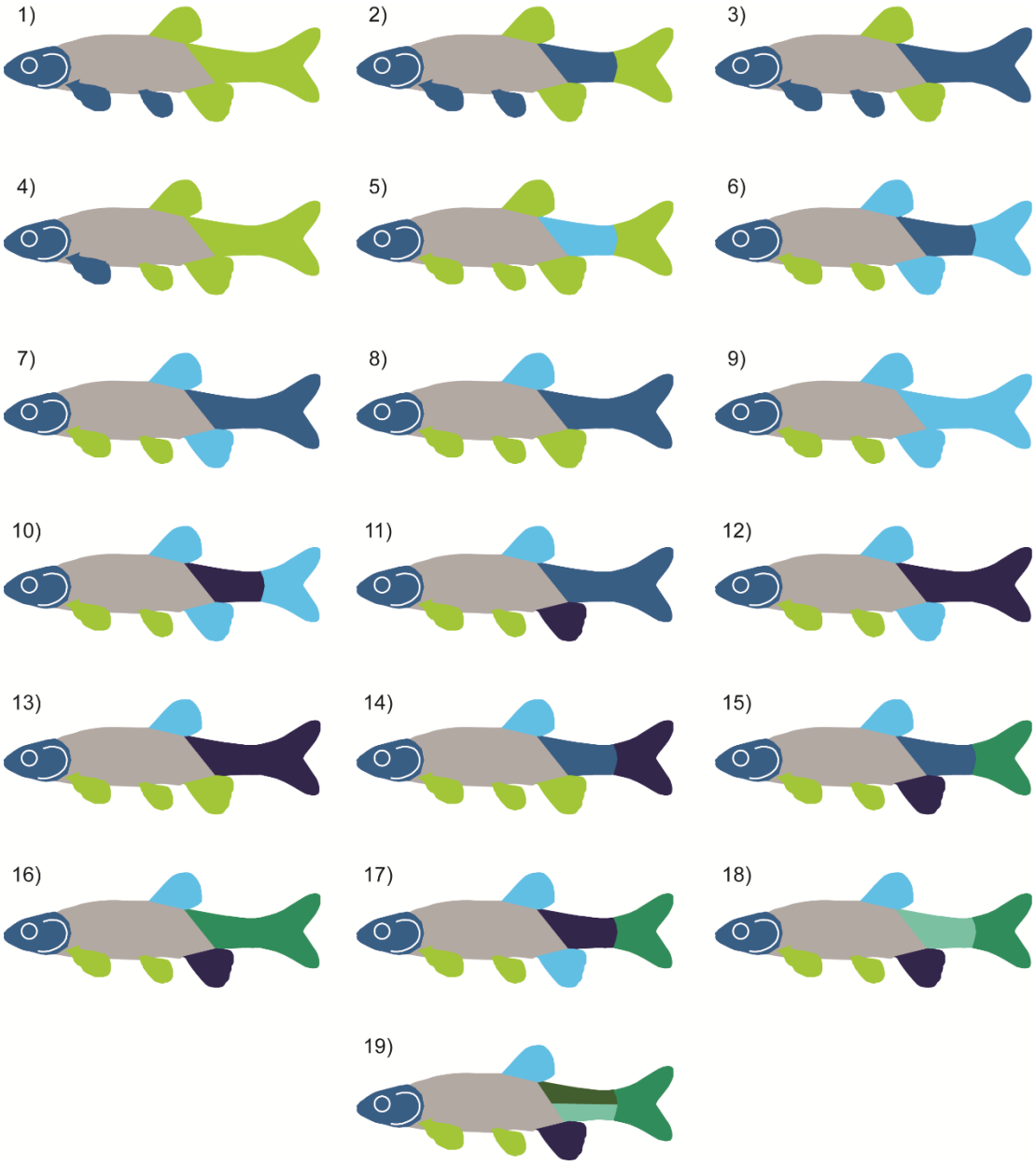

Figure 11: Graphical representation of the 19 *a priori* hypotheses of modularity. Regions of the body sharing the same coloration pattern form putative variational modules. See Table 8 for precise description of hypotheses.

Table 8: Description of the 19 *a priori* hypotheses of modularity. The numbers in parentheses refer to the landmarks and semi-landmarks included in each partition.

Hypothesis	Description of modular partitions
1	head + paired fins (1:5, 12:32, 67:69) median fins + tail (6:11, 33:66, 70:105)
2	head + paired fins + tail (1:5, 12:32, 67:105) median fins (6:11, 33:66)
3	head + caudal fin + paired fins + tail (1:5, 8:9, 12:14, 15:32, 41:58, 67:105) dorsal + anal fins (6:7, 10:11, 33:40, 59:66)
4	head + pectoral fins (1:5, 13:14, 15:32, 67:69) median fins + pelvic fins + tail (6:12, 33:66, 70:105)
5	head (1:5, 15:32) fins (6:14, 33:69) tail (70:105)
6	head + tail (1:5, 15:32, 70:105) median fins (6:11, 33:66) paired fins (12:14, 67:69)
7	head + tail + caudal fin (1:5, 8:9, 15:32, 41:58, 70:105) dorsal + anal fins (6:7, 10:11, 33:40, 59:66) paired fins (12:14, 67:69)
8	head + tail + caudal fin (1:5, 8:9, 15:32, 41:58, 70:105) dorsal fin (6:7, 33:40) ventral fins (10:14, 59:69)
9	head (1:5, 15:32) median fins + tail (6:11, 33:66, 70:105) paired fins (12:14, 67:69)
10	head (1:5, 15:32) median fins (6:11, 33:66) paired fins (12:14, 67:69) tail (70:105)
11	head + tail + caudal fin (1:5, 8:9, 15:32, 41:58, 70:105) dorsal fin (6:7, 33:40) anal fin (10:11, 59:66) paired fins (12:14, 67:69)
12	head (1:5, 15:32) dorsal + anal fins (6:7, 10:11, 33:40, 59:66) tail + caudal fin (8:9, 41:58, 70:105) paired fins (12:14, 67:69)
13	head (1:5, 15:32) dorsal fin (6:7, 33:40)

Hypothesis	Description of modular partitions
	tail + caudal fin (8:9, 41:58, 70:105)
	ventral fins (10:14, 59:69)
14	head + tail (1:5, 15:32, 70:105)
	dorsal fin (6:7, 33:40)
	caudal fin (8:9, 41:58)
	ventral fins (10:14, 59:69)
15	head + tail (1:5, 15:32, 70:105)
	dorsal fin (6:7, 33:40)
	caudal fin (8:9, 41:58)
	anal fin (10:11, 59:66)
	paired fins (12:14, 67:69)
16	head (1:5, 15:32)
	dorsal fin (6:7, 33:40)
	tail + caudal fin (8:9, 41:58, 70:105)
	anal fin (10:11, 59:66)
	paired fins (12:14, 67:69)
17	head (1:5, 15:32)
	dorsal + anal fins (6:7, 10:11, 33:40, 59:66)
	caudal fin (8:9, 41:58)
	paired fins (12:14, 67:69)
	tail (70:105)
18	head (1:5, 15:32)
	dorsal fin (6:7, 33:40)
	caudal fin (8:9, 41:58)
	anal fins (10:11, 59:66)
	paired fins (12:14, 67:69)
	tail (70:105)
19	head (1:5, 15:32)
	dorsal (6:7, 33:40)
	caudal fin (8:9, 41:58)
	anal fins (10:11, 59:66)
	paired fins (12:14, 67:69)
	upper tail (70:87)
	lower tail (88:105)

2.4.4.2 *Distance-matrix method*

The distance-matrix method, introduced by Monteiro et al. (2005), produces a correlation matrix between the shapes of subsets of landmarks. To obtain this matrix,

the coordinates are partitioned into subsets corresponding to hypothesized modules, or parts of modules. In the present case, the coordinates are partitioned into head, dorsal fin, caudal fin, anal fin, paired fins, dorsal tail outline, and ventral tail outline. If the partitions are individually superimposed after partitioning, the information about relative size and position within the body is removed from the data, leaving only information about shape. Alternatively, if they are superimposed only prior to partitioning, the information about relative size and position remains in the data. Pairwise Procrustes distances are calculated between all specimens (for each partition) and the matrix correlations between these pairwise distance matrices are then calculated, yielding a correlation matrix that can be analyzed by conventional methods for studies of modularity.

One method to test hypotheses of modularity is to analyze the correlation between this observed correlation matrix and those expected under the *a priori* hypotheses. To predict the matrices of expected correlations, a value of "1" is assigned to the cells if two partitions are expected to belong to a module, and a value of "0" when they are in separate modules (Cheverud et al. 1989; Cheverud et al. 1991; Ackermann and Cheverud 2000; Zelditch et al. 2008; Zelditch et al. 2009). The observed and expected matrices are compared by a Mantel test (Mantel 1967), testing the null hypothesis of no structural similarity between two matrices (Cheverud et al. 1989; Cheverud et al. 1991).

Modularity can also be assessed by graphical modeling, which evaluates the goodness-of-fit of models predicting correlations between two modules, conditional on all variables (here, the partitions) in the data. The aim is to reconstruct the observed covariance using as few "edges" as possible, with edges between variables ("nodes") representing conditionally dependent traits (Whittaker 1990; Edwards 1995; Lauritzen 1996; Edwards 2000; Magwene 2001, 2009; Zelditch et al. 2009). The model is fit using maximum-likelihood. Because models differ in the number of fixed parameters,

their relative fit can be assessed by the Akaike Information Criterion (AIC) (Akaike 1974).

2.4.4.3 *Minimum deviance method*

Instead of fitting models to a correlation matrix between partitions, this method fits models to the covariance matrix of landmark coordinates. The fit of the hypotheses is assessed through the standardized gamma statistic (γ*), a measure of the deviance between the model and the data (Richtsmeier et al. 2005; Márquez 2008). For the hypotheses, modules comprising subsets of landmarks are made statistically independent by placing them into orthogonal subspaces; intramodular covariances are estimated from the data (Márquez 2008). The null hypothesis is that the difference between the observed and expected covariance matrices is no greater than expected by chance; thus, a low *p*-value indicates that the model fits the data poorly (Parsons et al. 2012). The best fitting model is the one that deviates least from the data taking into account the number of fixed parameters. The γ* is scaled as a function of the maximum γ value (calculated from a null model of no integration), and scaled a second time to account for the number of fixed parameters (Márquez 2008). This last step is performed by regressing the γ values on the number of fixed parameters, since both are linearly related (Márquez 2008). Unfortunately, there is no method for statistically comparing these γ* values.

2.4.4.4 *Escoufier's RVs*

Escoufier's RV coefficient (1973) provides a measure of the covariation between partitions (hypothesized modules) relative to the covariance within them (Klingenberg 2009). If the modules are correctly delimited, the covariance between the two partitions should be lower than any other alternative partitioning because all of the alternatives will contain landmarks that covary. These alternative partitions are constructed so that

all have the same number of modules and the same number of landmarks *per* module (Klingenberg 2008, 2009). A null distribution of RVs is generated by randomly reassigning the landmarks and semi-landmarks into the same number of partitions as predicted by the hypothesis, each partition is also constrained to contain the same number of landmarks as in the hypothesis. The RV value obtained for the hypotheses is then compared to the null distribution to assess statistical significance; the hypothesis of modularity is supported when the covariance between hypothesized modules is lower than expected by chance (Klingenberg 2009).

2.4.4.5 A posteriori *hypotheses*

Hypotheses of modularity were also generated by heuristic searches for the best-fitting models. A heuristic search for the graphical model with the lowest deviance was performed by adding and removing edges one at a time. The search was performed bidirectionally, meaning that it toggles between backwards (removing edges) and forwards (adding edges) until no further edges can be removed or added in either direction (Edwards 2000). Furthermore, the search was coherent in that when the removal of an edge was rejected at any step in the process, it was subsequently fixed in the model (Edwards 2000).

A heuristic search was also performed using the minimum deviance method results. This is done by re-combining individual modules from the *a priori* hypotheses and performing a comprehensive search of all possible combinations (Márquez 2008), as implemented in Mint (Márquez 2014). In this procedure, modules are allowed to partially overlap but hypotheses with nested modules cannot be tested. These *a posteriori* models can then be ranked relative to the *a priori* ones.

2.4.4.6 *Software*

Landmarks and semi-landmarks were digitized with tpsDig2 (Rohlf 2013b) and superimposed using the package geomorph (Adams and Otarola-Castillo 2013) for R (R Core Team 2014). For the distance-matrix method, the observed correlation matrices were generated using a script developed by Adam Rountrey (available as supplementary material for Zelditch et al. (2012), at http://booksite.elsevier.com/9780123869036/functions.php), while the Mantel test was performed using the package vegan (Oksanen et al. 2013) in R. Graphical modeling was completed in MIM (Edwards 2004) and in R using the package ggm (Marchetti et al. 2014). The minimum deviance method was carried out using the program Mint (Márquez 2014). Escoufier's RV method was performed in R, as implemented in the geomorph package (Adams and Otarola-Castillo 2013).

2.5 Results

Results differed according to the methods that were used to test hypotheses of modularity (Tables 9 to 12). Because there is no procedure to statistically weight the global support for our hypotheses across methods, results are presented for each of the methods separately. In the distance-matrix approach, two different analyses were used to test hypotheses of modularity; results differed between Mantel tests and graphical modeling and so these are also presented separately. Moreover, differences in the results between semi-landmark superimposition approaches are compared for each analysis.

Table 9: Results of statistical analyses of modularity for the zebrafish (*Danio rerio*) using minimum bending energy for semi-landmark superimposition.

Hypothesis	Graphical modeling		Minimum deviance		Mantel test		RV's	
	Deviance	ΔAIC	γ*	*p*	Mantel statistic	*p*	RV	*p*
1	61.55	0	-0.338	1	0.293	0.152	0.571	1e-04
2	148.84	83.28	-0.101	0	-0.265	1	0.790	7e-04
3	130.98	69.43	0.021	0.001	-0.191	0.726	0.776	0.0105
4	NA	NA	-0.340	1	NA	NA	0.574	1e-04
5	175.83	106.28	-0.207	0	-0.300	0.928	0.603	1e-04
6	154.95	83.40	-0.142	0	0.064	0.393	0.406	1e-04
7	137.14	67.58	-0.037	0	0.260	0.167	0.410	1e-04
8	131.46	61.90	-0.025	0.001	0.353	0.092	0.426	1e-04
9	66.05	2.50	-0.359	1	0.388	0.191	0.332	1e-04
10	185.56	110.01	-0.236	0	0.011	0.395	0.443	1e-04
11	138.07	66.52	-0.025	0.001	0.447	0.089	0.327	1e-04
12	184.72	109.17	-0.199	0	0.104	0.277	0.461	1e-04
13	179.05	103.49	-0.186	0	0.215	0.184	0.467	1e-04
14	197.35	121.80	-0.098	0	0.077	0.318	0.486	1e-04
15	203.97	126.41	-0.098	0	0.187	0.234	0.400	1e-04
16	185.66	108.11	-0.186	0	0.343	0.178	0.390	1e-04
17	233.64	154.09	-0.204	0	-0.130	0.7	0.519	1e-04
18	234.58	153.03	-0.192	0	0.193	0.217	0.525	1e-04
19	266.63	183.08	-0.213	0	NA	NA	0.542	1e-04

Table 10: Results of statistical analyses of modularity for the zebrafish (*Danio rerio*) using minimum chord distance for semi-landmark superimposition.

Hypothesis	Graphical modeling		Minimum deviance		Mantel test		RV's	
	Deviance	ΔAIC	γ*	*p*	Mantel statistic	*p*	RV	*p*
1	55.75	0	-0.289	0.963	0.301	0.145	0.496	1e-04
2	148.26	88.51	-0.092	0	-0.131	0.753	0.759	0.0044
3	160.45	104.70	0.074	0	-0.111	0.574	0.816	0.1375
4	NA	NA	-0.303	0.997	NA	NA	0.485	1e-04
5	166.09	102.34	-0.226	0	-0.108	0.607	0.529	1e-04
6	153.89	88.14	-0.131	0	0.163	0.199	0.396	1e-04
7	167.83	104.08	0.022	0	0.252	0.169	0.425	1e-04
8	157.88	94.13	0.002	0	0.396	0.073	0.400	1e-04
9	59.25	1.50	-0.309	0.948	0.398	0.101	0.287	1e-04
10	181.29	111.54	-0.232	0	0.121	0.222	0.407	1e-04
11	167.83	102.08	0.015	0	0.459	0.079	0.299	1e-04
12	204.72	134.97	-0.142	0	0.190	0.218	0.438	1e-04
13	194.78	125.02	-0.162	0	0.363	0.064	0.408	1e-04
14	204.40	134.65	-0.118	0	0.277	0.134	0.444	1e-04
15	214.35	142.60	-0.105	0	0.370	0.150	0.374	1e-04
16	204.73	132.98	-0.149	0	0.467	0.039	0.351	1e-04
17	241.75	168.00	-0.200	0	0.050	0.404	0.497	1e-04
18	241.75	166.00	-0.207	0	0.486	0.051	0.473	1e-04
19	369.02	291.27	-0.228	0	NA	NA	0.563	1e-04

Table 11: Results of statistical analyses of modularity for the Northern redbelly dace (*Chrosomus eos*) using minimum bending energy for semi-landmark superimposition.

Hypothesis	Graphical modeling		Minimum deviance		Mantel test		RV's	
	Deviance	**ΔAIC**	**γ***	***p***	**Mantel statistic**	***p***	**RV**	***p***
1	119.85	0	-0.271	0.833	0.117	0.379	0.701	1e-04
2	202.55	78.70	-0.123	0	-0.259	0.980	0.836	2e-04
3	171.33	51.48	0.018	0.002	-0.121	0.612	0.820	0.0015
4	NA	NA	-0.272	0.903	NA	NA	0.708	1e-04
5	239.60	111.75	-0.269	0.004	-0.236	0.892	0.693	1e-04
6	236.60	106.75	-0.126	0	-0.005	0.499	0.587	1e-04
7	205.69	77.85	0.021	0	0.266	0.129	0.579	1e-04
8	177.66	49.81	0.040	0	0.461	0.056	0.536	1e-04
9	143.29	21.44	-0.277	0.726	0.194	0.275	0.529	1e-04
10	293.06	159.21	-0.238	0	-0.060	0.585	0.647	1e-04
11	220.36	90.51	0.073	0	0.443	0.125	0.531	1e-04
12	277.81	143.97	-0.157	0	0.116	0.281	0.662	1e-04
13	249.78	115.93	-0.136	0	0.351	0.076	0.619	1e-04
14	290.48	156.63	-0.045	0	0.095	0.319	0.643	1e-04
15	333.18	197.33	-0.012	0	0.057	0.369	0.634	1e-04
16	292.48	156.63	-0.103	0	0.344	0.147	0.618	1e-04
17	374.97	237.12	-0.177	0	-0.258	0.873	0.732	1e-04
18	389.64	249.79	-0.125	0	-0.005	0.502	0.735	1e-04
19	425.01	283.17	-0.160	0	NA	NA	0.735	1e-04

Table 12: Results of statistical analyses of modularity for the Northern redbelly dace (*Chrosomus eos*) using minimum chord distance for semi-landmark superimposition.

Hypothesis	Graphical modeling		Minimum deviance		Mantel test		RV's	
	Deviance	**ΔAIC**	**γ***	***p***	**Mantel statistic**	***p***	**RV**	***p***
1	103.41	0	-0.222	0.564	0.290	0.235	0.643	1e-04
2	139.85	32.44	-0.098	0	-0.077	0.631	0.756	3e-04
3	154.61	51.20	0.039	0.001	-0.117	0.720	0.797	0.0334
4	NA	NA	-0.224	0.631	NA	NA	0.679	2e-04
5	184.32	72.92	-0.237	0	-0.072	0.599	0.647	1e-04
6	174.26	60.86	-0.103	0	0.183	0.218	0.501	1e-04
7	190.85	79.45	0.045	0	0.221	0.183	0.513	1e-04
8	179.29	67.88	0.062	0	0.312	0.121	0.534	1e-04
9	111.41	6.00	-0.236	0.481	0.473	0.119	0.424	1e-04
10	212.67	95.27	-0.206	0	0.280	0.136	0.543	1e-04
11	203.89	90.49	0.086	0	0.376	0.148	0.482	1e-04
12	244.99	127.58	-0.116	0	0.252	0.158	0.563	1e-04
13	233.42	116.02	-0.098	0	0.361	0.078	0.587	1e-04
14	264.22	146.81	-0.029	0	0.088	0.360	0.619	1e-04
15	288.82	169.42	-0.006	0	0.163	0.349	0.565	1e-04
16	258.02	138.62	-0.075	0	0.469	0.027	0.537	1e-04
17	314.19	192.79	-0.151	0	0.064	0.384	0.666	1e-04
18	327.23	203.83	-0.110	0	0.396	0.057	0.694	1e-04
19	411.49	285.94	-0.140	0	NA	NA	0.731	1e-04

2.5.1 Distance-Matrix Method

2.5.1.1 *Mantel test*

When semi-landmarks are superimposed by the bending-energy criterion, none of the matrices representing the expected ("target") correlation matrices are significantly correlated to the observed correlation matrix. The best-supported model for *D. rerio* is hypothesis 11 predicting that the dorsal and anal fins are independent of each other, that the head is integrated with the tail region and that the paired fins form a module. The next best-supported hypothesis for *D. rerio*, hypothesis 8, differs from hypothesis 11 only in that it proposes that the paired fins form a ventral fins module including the anal fin. Although this is the second-best fitting model for *D. rerio*, it is the best-fitting one for *Chrosomus eos*. The second best-fitting model for *C. eos* is hypothesis 13 which differs from hypothesis 8 only in that the head is not integrated with the tail. Hypothesis 11, which was the best fitting model for *D. rerio*, is the third best-fitting for *C. eos*.

Using the minimum chord distance criterion instead, one of the hypothesized target matrices is significantly correlated to the observed correlation matrices. Additionally, hypothesis 16 is best-supported for both species. This hypothesis predicts that most individual partitions are modules, with the exception of the tail and caudal fin that are combined in the same module. The next best-supported hypothesis (hypothesis18) differs from the latter only in that the outline of the tail and the caudal fin are each separate modules.

2.5.1.2 *Graphical modeling*

For *D. rerio*, the two best-fitting models, assessed by graphical modeling, are hypotheses 1 and 9, both predicting that the tail region, including the bases of the dorsal and anal fins, form a module. They differ however in the patterns of integration of the

head and paired fins: according to hypothesis 1 the paired fins form a module which includes the head, while hypothesis 9 proposes that the paired fins and the head are separate modules. The two models fit the data for *D. rerio* equally well regardless of the superimposition method. Both hypotheses are also the highest ranking for *C. eos* although the difference in AIC between them is larger.

2.5.2 Minimum Deviance Method

Assessed for their fit to the covariance matrix of landmarks, the best-fitting models are the same two that were selected by graphical modeling, hypotheses 1 and 9. Hypothesis 4 also fits well and differs from hypotheses 1 and 9 in its expectations for the paired fins: the pectoral fins and the head form one module, while the pelvic fins and posterior trunk and tail form another.

2.5.3 Escoufier's RVs

The RV values for the 18 hypotheses range from 0.29 to 0.79 for *D. rerio*, and from 0.42 to 0.84 for *C. eos*. In all cases, the values are statistically significant, meaning that even the highest RVs are low relative to the distribution obtained by randomly partitioning the data. For *D. rerio*, the hypotheses with the lowest RV values are hypotheses 11, 16 and 9. These hypotheses show integration within the head and integration within the tail region. The three hypotheses also agree that the paired fins form a module independent from the rest of the body. However, hypotheses 11 and 16 exclude the base of the dorsal and anal fins from the tail module; instead they each form their own modules. Furthermore, in hypothesis 11, the head and the tail are part of the same module while in hypothesis 16 they are separate modules. As for *C. eos*, the best-fitting models also include hypotheses 11 and 9, while a third hypothesis depends on the superimposition method. When semi-landmarks are superimposed by the bending energy criterion, the third best-fitting model is hypothesis 8, whereas it is

hypothesis 6 when semi-landmarks are superimposed by the chord distance criterion. According to both hypotheses, the paired fins together form a module but hypothesis 8 supports that this module also includes the anal fin.

2.5.4 *A Posteriori* Results

2.5.4.1 *Graphical modeling*

More modules were detected by a heuristic search for the best graphical model when the partitions were superimposed separately. In striking contrast, if the landmarks are superimposed only prior to partitioning, no partitions are conditionally independent. That contrast between results suggests that information on fin positioning, which is lost when separately superimposing the partitions, is important to the morphological integration of the body. When separately superimposed by the bending energy criterion, the dorsal fin is conditionally independent of all other partitions in both species, as well as the paired fins in *D. rerio*. When instead partitions are superimposed by the chord distance criterion, only the paired fins form a module in *D. rerio*.

2.5.4.2 *Minimum deviance method*

Combining modules of *a priori* hypotheses and assessing these combinations by their γ^* values (Figure 12), the best-fitting models show absence of integration within the head. The tail region, including the bases of the dorsal and anal fins, is still recognized as a module, but models with strikingly different patterns of integration for the paired fins appear to fit equally well, differing by less than 0.002 in γ^* values for *D. rerio*. One of these *a posteriori* hypotheses has the paired fins forming a module, another shows no integration within the pectoral fins while the pelvic fins form a module with the posterior trunk and tail, and yet another shows no integration at all in the paired

fins. These *a posteriori* results do not support the hypothesis that the paired fins form a variational module.

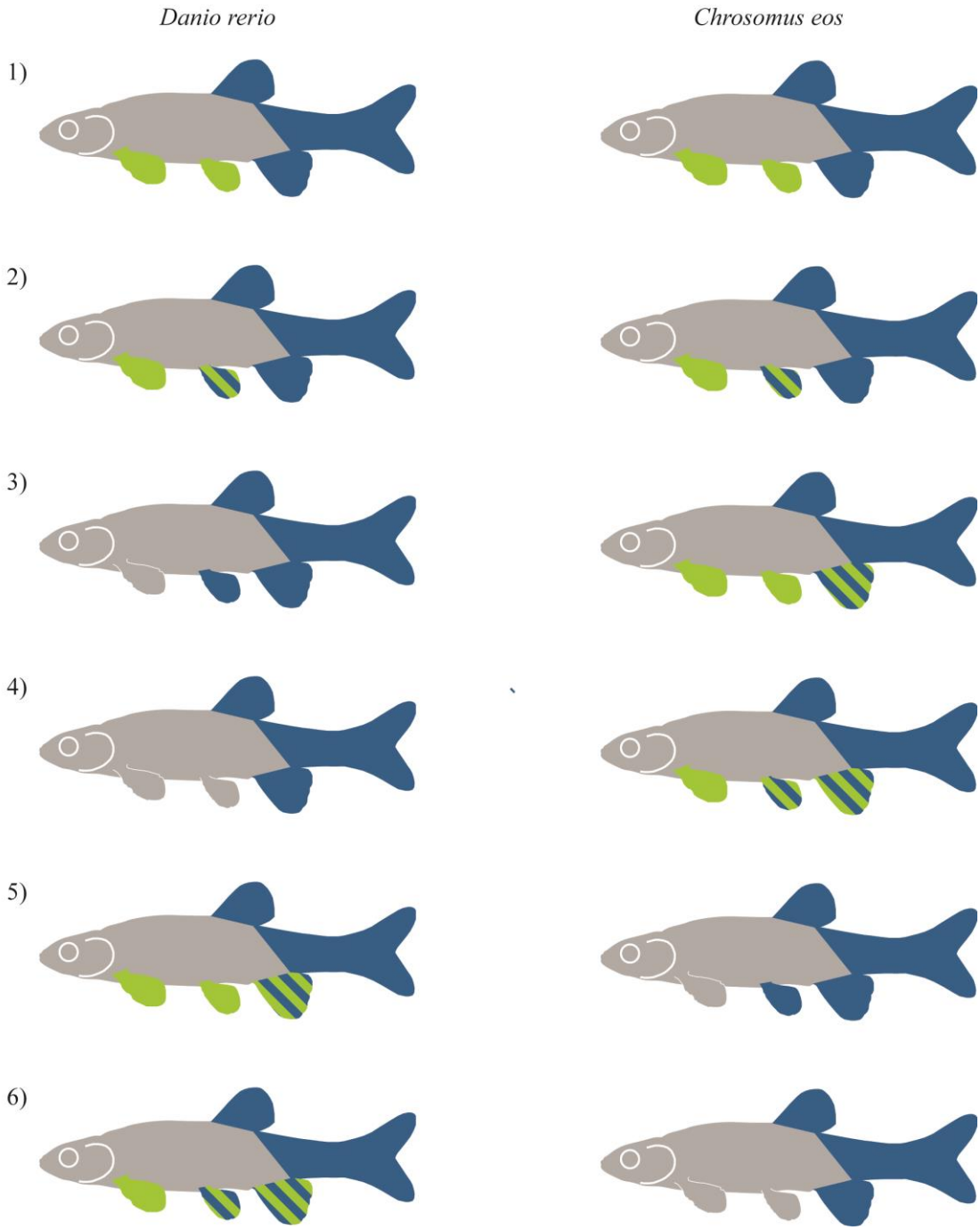

Figure 12: Graphical representations of the six best fitting *a posteriori* hypotheses of modularity using the minimum deviance method. For each specie, hypotheses are ordered based on the γ* value. Regions of the body sharing the same coloration pattern form putative variational modules. Regions where modules overlapped are shown with a hatched pattern.

2.6 Discussion

In this study, we investigated patterns of morphological integration in two species of cyprinid fishes for the purpose of identifying variational modules of fin positioning along the body axis. Two of our initial expectations were that (1) the dorsal and anal fins would form a variational module, and (2) the pectoral and pelvic fins would form a paired fins variational module. Most of the best supported hypotheses do suggest that the dorsal and anal fins are part of an integrated unit, but one that also includes the outline of the tail and the caudal fin. Consequently, the entire posterior trunk and tail region appears to constitute a single variational module. The best-supported hypotheses also indicate that the paired fins are integrated but the results of the heuristic searches provide less support for that hypothesis. Most of the best-fitting *a priori* hypotheses also supported the head as constituting a module but again the results from the heuristic searches suggest that there is no need to postulate integration of the head region; models lacking that integration fit as well as those that include it. In light of the diversity of methods that we used to test our hypotheses, it is important to note that the best-fitting hypotheses tend to differ across methods. Two of the methods yield similar results: graphical modeling applied to the correlations among partitions, and the standardized γ statistic obtained by fitting models to covariance matrices of landmark coordinates. In contrast, when models predicting correlations among partitions are assessed by the Mantel test and when models fit to covariance matrices are assessed by Escoufier's RVs, the best-fitting hypotheses differ not only from each other, but also from those that are well supported by the other two approaches. Nevertheless, for each method, the hypotheses that fit best are generally the same for both species, suggesting that

patterns of morphological integration are phylogenetically conserved. Of course, a rigorous demonstration of phylogenetic conservatism would require a larger sampling of species.

There is an important distinction among the four approaches used to investigate modularity, which is the concept of modularity that is tested. What makes modularity most relevant to evolutionary theory is the relationship between evolvability and the quasi-independence of phenotypic units, allowing them to be individually modified without interfering with others (Wagner 1996; Wagner and Altenberg 1996; Hansen 2003; Hansen et al. 2003). In this sense, the graphical modeling approach is particularly appealing because it tests for conditional independence (Whittaker 1990; Edwards 1995; Lauritzen 1996; Edwards 2000; Magwene 2001, 2009). The use of the standardized γ statistic to assess the fit of models to covariance matrices of landmarks also implies evolvability because modules are placed in orthogonal subspaces (Márquez 2008). Consequently, a model will fit well only if modules are independent of each other (Márquez 2008). The quasi-independence of modules is not necessary for a hypothesis of modularity to fit well as judged by the other two methods. Modules delimited by finding the minimum Escoufier's RV between partitions can be highly integrated with each other so long as the intra-modular covariances are higher. The Mantel test similarly does not test for conditional independence between modules, just proportionality between the observed and expected matrices. The two matrices may be proportional even if correlations between modules are high providing that the correlations between modules are consistently lower than those within modules. For these reasons, we focus on the results from graphical modeling of the correlations between distance matrices and the minimum deviance assessment of landmark covariance matrices.

The *a priori* hypotheses that we set out to test are inspired by a growing body of evidence of fin developmental modularity across different groups of fishes. The

expectation of a dorsal and anal fin module is based largely on the proposal that, in actinopterygians, these two fins originally shared both positioning and patterning modules (Mabee et al. 2002). Median fin positioning modules have also been suggested for chondrichthyan taxa, as exemplified in the catshark (*Scyliorhinus canicula*) where the position of the dorsal and anal fins are specified by patterns of expression of *Hoxd* genes, pointing towards the involvement of a developmental module (Freitas et al. 2006). Likewise, median fin patterning modules have been identified across a wide range of fish taxa. Similarities between dorsal and anal fins in the development of skeletal support elements have been observed in both actinopterygian and sarcopterygian species, suggesting that the dorsal and anal fins patterning modules might have been inherited from a common osteichthyan ancestor prior to the split of these two groups (Cloutier 2010). An additional median fins developmental module has been discussed for the caudal fin based on conserved developmental sequences and similarities in plastic responses in the Arctic char (*Salvelinus alpinus*) (Grünbaum et al. 2012). Moreover, there is also strong evidence for developmental modularity of the paired fins. Both structural (Bemis and Grande 1999) and developmental similarities (Freitas et al. 2006; Abe et al. 2007; Crotwell and Mabee 2007; Freitas et al. 2007; Freitas et al. 2014) suggest that paired fins might have originated from a reiteration of developmental module(s) initially associated with the median fins. Additionally, evidence from the fossil record shows that the pectoral fins appeared first among jawless fishes, followed by the pelvic fins, which originated in stem gnathostomes (Coates 1993, 1994; Coates and Cohn 1998). Furthermore, pectoral and pelvic fins are hypothesized to be condensations from a continuous pair of lateral finfolds (Balfour 1876; Thacher 1877; Balfour 1878; Mivart 1879; Balfour 1881; Goodrich 1906; Tanaka et al. 2002), implying similarities in their developmental mechanisms that predict similar morphologies, at least in primitive gnathostomes. On the other hand, pelvic fins can be modified independently of the pectoral fins and vice versa, suggesting that both sets of paired fins can be considered as separate modules (Coates and Cohn 1998; Hanke and Wilson 2006; Hall 2010).

Despite this wealth of evidence for fin developmental modularity, our results provide only weak support for the existence of fin variational modules. Contrary to our expectations of a dorsal-anal fin module, we found that the entire posterior trunk and tail, including bases of all three median fins, is integrated. Such a pattern of integration might be explained by locomotion kinematics in that both the zebrafish (Plaut and Gordon 1994) and Northern redbelly dace (T. Grünbaum, pers. comm.) employ subcarangiform locomotion. Subcarangiform swimming involves undulations of the posterior trunk and tail that are transmitted towards the caudal fin for propulsion (Webb 1975; Lindsey 1978; Sfakiotakis et al. 1999). Thus the requirements of swimming could explain why this entire posterior region of the body, including the bases of the dorsal and anal fins, should be functionally integrated. This suggests that functional integration can overwrite the expectations of variational modularity inferred from developmental patterns.

Another hypothesis based on strong evidence for developmental modularity was that the pectoral and pelvic fins would be integrated, forming a paired fins variational module. This hypothesis is well supported in many of the best-fitting models from the *a priori* analyses but not by results of heuristic searches, which show equal support for different patterns of integration of paired fins. This suggests that paired fins integration is not what determines whether a model will fit well. Instead, it is the integration of the head (or lack thereof), and that of the trunk and tail, that are more consequential. Yet heuristic searches also demonstrate that when only the shapes of the partitions are analyzed, thereby excluding information about relative position and size, the paired fins are conditionally independent for *D. rerio*. This finding at least weakly supports the hypothesis of a pectoral-pelvic fins variational module. The rationale for expecting a paired fins variational module is that the fore- and hindlimbs of tetrapods are a classic example of serial homology and modularity (Shubin et al. 1997; Hallgrímsson et al. 2002; Young and Hallgrímsson 2005; Young et al. 2010). One hypothesis is that the

pelvic fins originated from a duplication of the pectoral fins and as such, the two might have primitively shared a positioning module. Perhaps this paired fins positioning module has become decoupled, a process that has also been proposed to explain how the basal condition of symmetrical positioning of dorsal and anal fins relative to the antero-posterior body axis tends to be lost in more derived actinopterygians (Mabee et al. 2002). Further evidence for decoupling of paired fins modules can also be found in the observation that pectoral and pelvic fins are frequently modified or lost independently from one another in both actinopterygians (Hall 2010) and sarcopterygians (Coates et al. 2002). In basal actinopterygians and chondrichthyans, the paired fins both have a ventral insertion but in derived actinopterygians, their relative positioning is much more variable, although there is a tendency for the pectoral fins to migrate laterally and dorsally, and pelvic fins to migrate anteriorly (Rosen 1982; Yamanoue et al. 2010). An investigation focusing on more basal taxa, closer to the node where the pelvic fins first appeared, might yield stronger evidence for the existence of a paired fins variational module.

Our failure to detect some of the expected modules might also be explained on methodological grounds, especially the impact of spatial contiguity of landmarks on covariances between them. Spatially contiguous landmarks are expected to covary more strongly than more distant ones (Adams et al. 2013). For instance, the base of the dorsal, anal and caudal fins are in direct continuity with the outline of the trunk and tail, and that might introduce covariance among those three fins. The situation is different for the paired appendages because the pectoral fins are closer to the head than they are to the pelvic fins, which are inserted ventrally about halfway between the pectoral and anal fins. The observation that hypotheses showing the paired fins forming an integrated unit are consistently well supported across methods might then indicate that they do form a variational module.

Perhaps the best explanation for the discrepancy between the expected and observed fin modules is that there is no simple one to one correspondence between developmental modules and variational modules. Many of the fin modules that we expected to find are deduced from molecular and developmental data (Ruvinsky and Gibson-Brown 2000; Crotwell et al. 2001; Mabee et al. 2002; Crotwell et al. 2004; Cloutier 2010; Tanaka and Onimaru 2012), while our analysis focused on variational modularity. Variational modules may differ from developmental modules because the combined effect of two or more of the latter on covariance patterns can partially overwrite each other (Hallgrímsson et al. 2009). Thus, the cumulative action of different modular processes during development, each affecting different combinations of traits, might result in an overall pattern of integration that obscures the boundaries among them (Hallgrímsson et al. 2009). The idea that developmental modularity leads to variational modularity, which, in turn, leads to evolutionary modularity is attractive. However, as we show here, developmental and variational modules need not correspond. Nevertheless, an idea worth investigating is that developmental modules, which are not as dependent on the vagaries of local population genetic structure, may be the units of evolutionary change.

CHAPITRE III

TÊTE, NAGEOIRES ET QUEUE : UNE ANALYSE COMPARATIVE DES PATRONS D'INTÉGRATION MORPHOLOGIQUE ET DE MODULARITÉ ENTRE LES ÉCHELLES MICRO- ET MACROÉVOLUTIVES

3.1 Résumé

Les lignées évolutives diffèrent fréquemment quant à l'ampleur de la disparité morphologique qui s'accumule au sein des espèces qu'elles contiennent. La capacité à générer de la disparité entre les espèces pourrait dépendre de propriétés variationnelles, par exemple l'évolvabilité de certains sous-ensembles de traits. La modularité peut influencer ces propriétés variationnelles en permettant des changements dans les taux ou dans les modalités d'évolution entre des structures. En utilisant une approche en morphométrie géométrique, les patrons d'intégration morphologique et de modularité évolutive ont été analysés pour un échantillon de 58 espèces d'actinoptérygiens couvrant un large spectre phylogénétique. Nous avons examiné l'hypothèse proposant que la modularité évolutive puisse influencer les taux d'évolution morphologique et la disparité entre les modules. Nous avons aussi vérifié si les patrons d'intégration morphologique qui avaient été observés à l'échelle microévolutive correspondent à ceux observés à l'échelle macroévolutive. Parmi les hypothèses les mieux supportées par les méthodes mettant l'emphase sur la quasi-indépendance des modules, nous avons observé que les taux d'évolution morphologique différaient entre les modules. Ceci suggère que la modularité peut promouvoir la disparification morphologique au sein des clades en permettant des taux d'évolution morphologique distincts entre les modules. Nous avons observé certaines différences entre les patrons d'intégration morphologique et de modularité aux échelles micro- et macroévolutives. Les patrons d'intégration morphologique observés à l'échelle macroévolutive pourraient

représenter une combinaison de plusieurs patrons d'intégration morphologique propres à certaines des lignées évolutives d'actinoptérygiens incorporées dans cette analyse.

Cet article, intitulé *Heads, Fins and Tails: A Comparative Analysis of Micro- and Macroevolutionary Patterns of Integration and Modularity in Fishes*, a été corédigé par moi-même ainsi que par Miriam L. Zelditch et Richard Cloutier. Cet article est en fin de préparation pour soumission dans le journal international *Evolution*. Le projet a été élaboré par Richard Cloutier et par moi-même. Les aspects méthodologiques de l'analyse des données ont été développés par Miriam L. Zelditch et par moi-même. En tant que premier auteur, mes contributions incluent notamment la revue de la littérature pertinente, la collection de la base de données de photographies de spécimen, la digitalisation des landmarks, la complétion des analyses et la production des figures et du matériel supplémentaire. J'ai rédigé la première version du manuscrit, et tous les auteurs ont contribué aux versions subséquentes.

Je tiens à remercier D. Nelson, gestionnaire des collections ichthyologiques du *University of Michigan Museum of Zoology*, pour son assistance lors de ma visite dans le but de photographier des spécimens. Sans son aide précieuse, j'aurais perdu de nombreuses heures à chercher des spécimens, considérant la taille impressionnante de cette collection de poissons. Je remercie aussi M. L. Zelditch et D. L. Swiderski pour m'avoir hébergé dans le cadre d'un stage en morphométrie géométrique à Ann Arbor (Michigan) au cours duquel l'essentiel des résultats de ce troisième chapitre ont été produits. Ce projet a été supporté financièrement en partie par le Conseil de Recherches en Sciences naturelles et en Génie du Canada (BESC-M et PGS-D octroyés à O. L.; NSERC Discovery Grant octroyé à R. C.) et par les Fonds de Recherche Nature et Technologies Québec (B1 octroyé à O. L.).

Head, Fins and Tail: A Comparative Analysis of Micro- and Macroevolutionary Patterns of Integration and Modularity in Fishes

3.2 Abstract

Evolutionary lineages often differ in the amount of morphological disparity that accumulates among the species that they contain. The ability to generate disparity across species may be linked to variational properties, such as the evolvability of some subsets of traits. Modularity may enhance these variational properties by allowing shifts in rates or in modes of evolution among structures. Using methods of geometric morphometry, we investigated patterns of morphological integration and modularity across several actinopterygian species spanning a wide phylogenetic spectrum. We investigated the hypothesis that evolutionary modularity can influence rates of morphological evolution and disparity across modules. We also verified if patterns of morphological integration that had been observed at the microevolutionary scale translated to the macroevolutionary scale. Among the best fitting hypotheses of modularity using methods emphasizing quasi-independence of modules, we found that rates of phenotypic evolution differed across modules. This suggests that modularity can promote morphological disparification among clades by allowing differing rates of phenotypic evolution across modules. We did not observe a one to one correspondence between patterns of integration and modularity at the micro- and macroevolutionary scales. Instead, patterns of morphological integration at the macroevolutionary scale could reflect a combination of several distinctive patterns specific to some of the actinopterygian lineages included in the analysis.

KEYWORDS: evolutionary modularity, morphological integration, morphological disparity, phenotypic evolution, evolutionary rates, actinopterygians, geometric morphometry, median fins, paired fins.

3.3 Introduction

Morphological disparity is not evenly distributed among radiating lineages (Gould 1989; Wainwright et al. 2004; Collar et al. 2005; Minelli 2016), or even among different parts of organisms (Linde-Medina et al. 2016). Differences in disparity among lineages can result from differences in ecological circumstances (Schluter 1996; Losos et al. 1997; Wainwright et al. 2004; Collar et al. 2005; Mahler et al. 2010; Collar et al. 2014) and/or to intrinsic variational properties (Vermeij 1973; Lewontin 1974; Raff 1996). Modularity is one of these properties that postulates that biological systems, whether at the molecular, organismal or ecological levels, can be decomposed into highly integrated component parts, which are termed modules (Wagner 1996; Winther 2001; Klingenberg 2008). These modules are subsets of traits that are internally strongly coherent and behave as quasi-independent units over development and/or evolution (Simon 1962; Magwene 2001; Müller 2007). Modularity is considered to be a variational property because it enables one part of a complex to evolve independently from others and thereby reach its optimal form without interfering with the adaptations of other parts (Bonner 1988; Raff 1996; Wagner 1996; Wagner and Altenberg 1996; Hansen 2003; Hansen et al. 2003; Hansen 2006; Hendrikse et al. 2007). This quasi-independence allowing some subsets of traits to evolve while others are fixed is known as conditional evolvability (Hansen 2003; Hansen et al. 2003; Hansen 2006). The expectation is that subsets of traits belonging to individual modules will evolve in a coordinated manner, whereas traits across modules will evolve quasi-independently (Wagner 1996; Gerhart and Kirschner 2007), thus potentially creating disparity among clades (West-Eberhard 2003; Sanger et al. 2012).

Modularity facilitates evolvability but this is not to say that hypothetical non-modular organisms could not evolve in different directions. The expectation is simply that more modular organisms will evolve more rapidly. A modular organization can allow for

higher rates of morphological evolution because it reduces interference across modules (Wagner 1996). Shifts in these rates of morphological evolution are hypothesized to influence the extent of morphological disparity that accumulates among radiating clades (Foote 1997; Harmon et al. 2003; Ackerly and Nyffeler 2004; O'Meara et al. 2006; Sidlauskas 2007, 2008; Denton and Adams 2015). Additionally, modularity can allow for different rates of morphological evolution among modules (Denton and Adams 2015).

There are different kinds of modules that can be categorized according to the types of processes that they are involved in. Developmental modules are generally defined as developmentally autonomous parts of an organism (Raff 1996; Bolker 2000; Wagner and Mezey 2004; Wagner et al. 2007). Variational modules refer to sets of phenotypic traits that are strongly integrated in their variation and quasi-independent of other sets due to the underlying patterns of expression of pleiotropic genes (Wagner and Altenberg 1996; Wagner and Mezey 2004; Wagner et al. 2007; Márquez 2008). Variational modules are studied by analyzing covariation patterns between quantitative traits (Olson and Miller 1958; Cheverud 1982, 1996b). A question that needs to be addressed is if these patterns of covariation at a microevolutionary scale translate to evolutionary covariation at a macroevolutionary scale. One hypothesis is that both variational and developmental modules can also become independent units of evolutionary change, making them evolutionary modules as well (Wagner 1996; Schlosser and Wagner 2004; Wagner and Mezey 2004). Another hypothesis is that evolutionary modules arise through the combined influence of genetic, developmental and functional integration (Brandon 1999; Klingenberg 2008; Sanger et al. 2012; Claverie and Patek 2013).

In this study focusing on the macroevolutionary consequences of modularity, we use actinopterygian fishes as a model system. Actinopterygians are a remarkably diverse group of fishes comprising over 30 000 living species (Nelson et al. 2016). This specific

diversity is coupled to high levels of morphological disparity, one aspect of which has to do with variations in fin configurations (Larouche et al. 2017). Indeed, many changes in modes of feeding and locomotion are associated with modifications of the structure, size, number and position of fins (Webb 1982; Lauder and Liem 1983; Webb 1984; Lauder and Drucker 2004). A previous investigation at a microevolutionary scale suggested that the dorsal and anal fins were functionally integrated with the posterior trunk and tail, and also showed some support for the pectoral and pelvic fins forming a paired fins variational module (Larouche et al. 2015). Here, we analyze evolutionary patterns of morphological integration and modularity across several actinopterygian lineages. We investigate the relationship between modularity and morphological disparity by verifying if there is a difference in evolutionary rates among modules. Our prediction is that modularity could facilitate shifts in rates of morphological evolution, and that increased rates of phenotypic evolution in some modules may lead to increased disparity across species for these modules. We also verify if patterns for variational modularity predict those for evolutionary modularity. Because the variation in fin positioning will be of a greater magnitude across species than within them, patterns of co-variation should be easier to detect. Consequently, we expected that the support for evolutionary modularity of the dorsal and anal fins, and of the pectoral and pelvic fins, would be greater than that which was obtained for variational modularity.

3.4 Methods

3.4.1 Sample

Morphological integration and hypotheses of evolutionary modularity were examined using a landmark-based geometric morphometry approach. We assembled a dataset of photographs of specimens from online repositories of catalogued collections, with additional photographs taken while visiting museum collections. It was assumed that the identification of specimens was correct, although some species' names were

Table 13: List of species sampled in this macroevolutionary analysis on patterns of morphological integration and evolutionary modularity.

No	Species in dataset	Family	Order
1	*Acipenser oxyrinchus*	Acipenseridae	Acipenseriformes
2	*Polyodon spathula*	Polyodontidae	Acipenseriformes
3	*Albula glossodonta*	Albulidae	Albuliformes
4	*Amia calva*	Amiidae	Amiiformes
5	*Oryzias hubbsi*	Adrianichthyidae	Beloniformes
6	*Strongylura strongylura*	Belonidae	Beloniformes
7	*Hyporhamphus acutus*	Hemiramphidae	Beloniformes
8	*Beryx decadactylus*	Berycidae	Beryciformes
9	*Holocentrus adscensionis*	Holocentridae	Beryciformes
10	*Ostichthys kaianus*	Holocentridae	Beryciformes
11	*Aulotrachichthys heptalepis*	Trachichthyidae	Beryciformes
12	*Gephyroberyx darwini*	Trachichthyidae	Beryciformes
13	*Hoplostethus cadenati*	Trachichthyidae	Beryciformes
14	*Barbourisia rufa*	Barbourisiidae	Cetomimiformes
15	*Alosa fallax*	Clupeidae	Clupeiformes
16	*Catostomus wigginsi*	Catostomidae	Cypriniformes
17	*Danio albolineatus*	Cyprinidae	Cypriniformes
18	*Pachypanchax omalonotus*	Aplocheilidae	Cyprinodontiformes
19	*Gambusia nobilis*	Poeciliidae	Cyprinodontiformes
20	*Elops hawaiensis*	Elopidae	Elopiformes
21	*Megalops atlanticus*	Megalopidae	Elopiformes
22	*Esox americanus*	Esocidae	Esociformes
23	*Umbra limi*	Umbridae	Esociformes
24	*Chanos chanos*	Chanidae	Gonorynchiformes

No	Species in dataset	Family	Order
25	*Gonorynchus greyi*	Gonorynchidae	Gonorynchiformes
26	*Kneria wittei*	Kneriidae	Gonorynchiformes
27	*Atractosteus spatula*	Lepisosteidae	Lepisosteiformes
28	*Ogilbia mccoskeri*	Bythitidae	Ophidiiformes
29	*Alepocephalus bairdii*	Alepocephalidae	Osmeriformes
30	*Galaxias maculatus*	Galaxiidae	Osmeriformes
31	*Microstoma microstoma*	Microstomatidae	Osmeriformes
32	*Holtbyrnia macrops*	Platytroctidae	Osmeriformes
33	*Arapaima gigas*	Arapaimidae	Osteoglossiformes
34	*Heterotis niloticus*	Arapaimidae	Osteoglossiformes
35	*Hiodon alosoides*	Hiodontidae	Osteoglossiformes
36	*Hiodon tergisus*	Hiodontidae	Osteoglossiformes
37	*Marcusenius ntemensis*	Mormyridae	Osteoglossiformes
38	*Paracanthurus hepatus*	Acanthuridae	Perciformes
39	*Meiacanthus grammistes*	Bleniidae	Perciformes
40	*Enneacanthus gloriosus*	Centrarchidae	Perciformes
41	*Chaetodon modestus*	Chaetodontidae	Perciformes
42	*Prognathodes carlhubbsi*	Chaetodontidae	Perciformes
43	*Cyprichromis leptosoma*	Cichlidae	Perciformes
44	*Coris nigrotaenia*	Labridae	Perciformes
45	*Pseudodax moluccanus*	Labridae	Perciformes
46	*Brockius striatus*	Labrisomidae	Perciformes
47	*Leiognathus equulus*	Leiognathidae	Perciformes
48	*Chromis ternatensis*	Pomacentridae	Perciformes
49	*Stegastes nigricans*	Pomacentridae	Perciformes
50	*Epinephelus howlandi*	Serranidae	Perciformes

No	Species in dataset	Family	Order
51	*Siganus doliatus*	Siganidae	Perciformes
52	*Toxotes jaculatrix*	Toxotidae	Perciformes
53	*Aphredoderus sayanus*	Aphredoderidae	Percopsiformes
54	*Polymixia japonica*	Polymixiidae	Polymixiiformes
55	*Sebastes mentella*	Sebastidae	Scorpaeniformes
56	*Nematogenys inermis*	Nematogenyidae	Siluriformes
57	*Poromitra crassiceps*	Melamphaidae	Stephanoberyciformes
58	*Bathophilus flemingi*	Stomiidae	Stomiiformes

updated to reflect the results of recent taxonomical investigations. The sample comprised 58 actinopterygian species from a wide phylogenetic spectrum (Table 13), with the constraint that they shared a similar fin configuration. This is because all specimens are required to share the same number of homologous landmarks (Zelditch et al. 2012). For the purpose of comparing the results of this macroevolutionary study with those of our previous analysis focusing on variational modularity (Larouche et al. 2015), we used fishes that had the same fin configurations as the zebrafish (*Danio rerio*) and the Northern redbelly dace (*Chrosomus eos*): all species analyzed have single dorsal and anal fins, a caudal fin, and both pectoral and pelvic fins. Species with fusions of some of the fins (e.g., dorsal and anal fins confluent with the caudal fin), those with more than one separate dorsal or anal fins, and those with extreme morphologies (e.g., Pleuronectiformes) were not included in the analyses.

3.4.2 Geometric morphometrics

To analyze fin-positioning, we placed nine landmarks at the fin insertion points and five additional landmarks were placed at the anterior limit of the rostrum, anterior and posterior limits of the eye and dorsal and ventral limits of the gill cover (Figure 13,

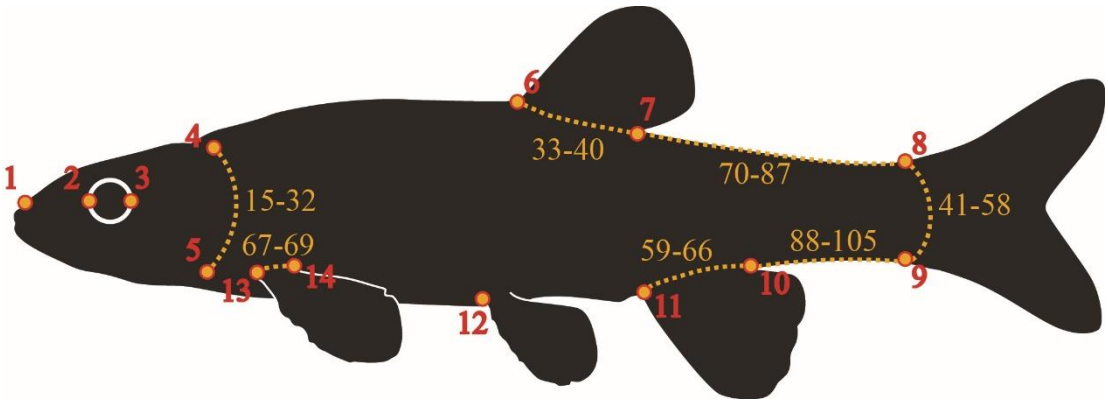

Figure 13: Illustration showing landmarks (numbered in red) and semi-landmarks (numbered in yellow) positioning scheme. See Table 14 for a description of landmark positions.

Table 14). A series of 55 semi-landmarks were used to provide additional information for curves along the body where landmarks could not be consistently positioned in homologous locations. Because the spacing between semi-landmarks is not arbitrary, semi-landmarks contain less information than landmarks but are nonetheless useful when the latter cannot fully capture the information about shape. Semi-landmarks were placed along the outline of the operculum, the base of each fin and the tail region, which we consider to be the posterior part of the body extending behind dorsal and anal fins and supporting the caudal fin.

Digitized coordinates were superimposed using a General Procrustes Analysis (Rohlf and Slice 1990). Semi-landmarks require an additional step to remove the variation owing to their arbitrary position along the curve. In a previous analysis, we found that semi-landmark superimposition method did not affect the results qualitatively (Larouche et al. 2015). Thus, in this case we used the criteria of minimum bending energy of the deformation between the target shape and the reference (mean) shape for the optimal semi-landmark superimposition (Green 1996; Bookstein 1997). This criteria evenly distributes the variance to all of the semi-landmarks along a curve, as

Table 14: Description of landmarks for the analyses of geometric morphometry.

No	Description of landmarks
1	Anterior limit of the rostrum
2	Anterior limit of the eye
3	Posterior limit of the eye
4	Dorsal limit of the operculum opening
5	Ventral limit of the operculum opening
6	Anterior insertion of the dorsal fin
7	Posterior insertion of the dorsal fin
8	Dorsal insertion of the caudal fin
9	Ventral insertion of the caudal fin
10	Posterior insertion of anal fin
11	Anterior insertion of the anal fin
12	Insertion of the pelvic fin
13	Dorsal insertion of the pectoral fin
14	Ventral insertion of the pectoral fin

opposed to the minimum chord distance which tends to redistribute much of the variance to the first and last semi-landmarks. Furthermore, in minimizing the chord distance, one assumption is that all of the semi-landmarks should be independent, which is obviously not the case. Considering the extensive morphological disparity in our macroevolutionary dataset of fishes, we made sure that the superimposition process did not produce distortions to the data. This is because the Procrustes superimposition projects the original data, which lies in a curved space, onto a linear space; distances between points that are far apart in curved space can become significantly shorter once projected onto a linear space (Zelditch et al. 2012). To verify if this effect was

significant we calculated the correlation between distances in tangent space (superimposed data) and those in shape space (original data). We obtained a correlation of 0.9998 indicating that the distances between shapes in shape space are not distorted in tangent space.

3.4.3 Taking into account phylogeny

We tested for the presence of phylogenetic signal in the dataset using the multivariate generalization of Blomberg's K statistic (Blomberg et al. 2003), which quantifies the amount of phylogenetic signal across traits and trees (Adams 2014a). We then used a Mantel test (Mantel 1967) to compare the evolutionary variance-covariance matrix to the non-phylogenetic covariance matrix of shape. This indicates if the structure of the shape data is significantly affected when phylogeny is taken into account. Some methods for testing evolutionary modularity or comparing evolutionary rates assume that the traits evolve under Brownian evolution (e.g., covariation ratio, evolutionary rates ratio). We estimated model parameters and compared the strength of support among the three most common evolutionary models, Brownian motion (BM; Felsenstein 1973; Felsenstein 1985), Ornstein-Uhlenbeck (OU; Hansen 1997; Butler and King 2004), and Early burst (EB; Harmon et al. 2010). We also used disparity through time (DTT) analyses as described in Harmon et al. (2003). In this approach, disparity is calculated as the average pairwise Euclidian distance between species, first for the entire phylogeny, and then for every subclade defined by a node on the tree. Mean disparity values are obtained for each of the nodes of the tree and these are used to generate a DTT plot. Departures of the DTT plots from a null model generated by simulations of character evolution under Brownian motion are then quantified using a morphological disparity index (MDI). Positive values for the MDI mean that most of the disparity is partitioned within subclades, which is indicative of a OU model, while negative values indicate that most of the disparity is partitioned between subclades, which is indicative of an EB model (Harmon et al. 2003; Harmon et al. 2010). The

phylogenetic context for these analyses was provided by a pruned version of a recently published time-calibrated actinopterygian phylogeny based on the partitioned maximum-likelihood analysis of nine nuclear gene sequences (Near et al. 2012).

3.4.5 Quantifying allometry

Actinopterygians are highly disparate in terms of body size, the total length of living species ranging from 7.9 mm (*Paedocypris progenetica*) to over 6 m (*Regalescus glesne*). Procrustes superimposition performs a geometric rescaling of the data but does not remove the allometric component that can be present (Zelditch et al. 2012). We tested for the covariance between shape and centroid size, taking phylogeny into account. Variation in shape is not explained by variation in size ($F = 0.75$, $p = 0.801$). Consequently, we did not standardize the data by removing the effect of size from the shape data.

3.4.6 Testing hypotheses of modularity

3.4.6.1 A priori *hypotheses*

A total of 24 *a priori* hypotheses of modularity were analyzed (Table 15). Most of these hypotheses of modularity are identical to those of our previous study focusing on variational modularity within two cyprinid species, *D. rerio* and *C. eos* (Larouche et al. 2015). Five additional hypotheses were added based on the results of a recently published analysis that had a similar landmark sampling scheme (Denton and Adams 2015) and the results of a study focusing on modularity and morphological disparity in fin configurations at a macroevolutionary scale (Larouche et al. 2017). These additional hypotheses were retroactively also analyzed for the *D. rerio* and *C. eos* datasets.

Table 15: Description of the 24 a priori hypotheses of modularity tested in this analysis on macroevolutionary patterns integration. The numbers in parentheses refer to the landmarks and semi-landmarks included in each partition (See Figure 13).

Hypothesis	Description of modular partitions
1	head + paired fins (1:5, 12:32, 67:69) median fins + tail (6:11, 33:66, 70:105)
2	head + paired fins + tail (1:5, 12:32, 67:105) median fins (6:11, 33:66)
3	head + caudal fin + paired fins + tail (1:5, 8:9, 12:14, 15:32, 41:58, 67:105) dorsal + anal fins (6:7, 10:11, 33:40, 59:66)
4	head + pectoral fin (1:5, 13:14, 15:32, 67:69) median fins + pelvic fin + tail (6:12, 33:66, 70:105)
5	head (1:5, 15:32) fins (6:14, 33:69) tail (70:105)
6	head + tail (1:5, 15:32, 70:105) median fins (6:11, 33:66) paired fins (12:14, 67:69)
7	head + tail + caudal fin (1:5, 8:9, 15:32, 41:58, 70:105) dorsal + anal fins (6:7, 10:11, 33:40, 59:66) paired fins (12:14, 67:69)
8	head + tail + caudal fin (1:5, 8:9, 15:32, 41:58, 70:105) dorsal fin (6:7, 33:40) ventral fins (10:14, 59:69)
9	head (1:5, 15:32) median fins + tail (6:11, 33:66, 70:105) paired fins (12:14, 67:69)
10	head (1:5, 15:32) median fins (6:11, 33:66) paired fins (12:14, 67:69) tail (70:105)

Hypothesis	Description of modular partitions
11	head + tail + caudal fin (1:5, 8:9, 15:32, 41:58, 70:105) dorsal fin (6:7, 33:40) anal fin (10:11, 59:66) paired fins (12:14, 67:69)
12	head (1:5, 15:32) dorsal + anal fins (6:7, 10:11, 33:40, 59:66) tail + caudal fin (8:9, 41:58, 70:105) paired fins (12:14, 67:69)
13	head (1:5, 15:32) dorsal fin (6:7, 33:40) tail + caudal fin (8:9, 41:58, 70:105) ventral fins (10:14, 59:69)
14	head + tail (1:5, 15:32, 70:105) dorsal fin (6:7, 33:40) caudal fin (8:9, 41:58) ventral fins (10:14, 59:69)
15	head + tail (1:5, 15:32, 70:105) dorsal fin (6:7, 33:40) caudal fin (8:9, 41:58) anal fin (10:11, 59:66) paired fins (12:14, 67:69)
16	head (1:5, 15:32) dorsal fin (6:7, 33:40) tail + caudal fin (8:9, 41:58, 70:105) anal fin (10:11, 59:66) paired fins (12:14, 67:69)
17	head (1:5, 15:32) dorsal + anal fins (6:7, 10:11, 33:40, 59:66) caudal fin (8:9, 41:58) paired fins (12:14, 67:69) tail (70:105)

Hypothesis	Description of modular partitions
18	head (1:5, 15:32) dorsal fin (6:7, 33:40) caudal fin (8:9, 41:58) anal fins (10:11, 59:66) paired fins (12:14, 67:69) tail (70:105)
19	head (1:5, 15:32) dorsal (6:7, 33:40) caudal fin (8:9, 41:58) anal fins (10:11, 59:66) paired fins (12:14, 67:69) upper tail (70:87) lower tail (88:105)
20	lower caudal peduncle (88:105) all other landmarks (1:87)
21	head + median fins + paired fins (1:69) caudal peduncle (70:105)
22	head + trunk (1:7, 10:40, 59:69) caudal peduncle and fin (8,9, 41:58, 70:105)
23	head (1:5, 15:32) all other landmarks (6:14, 33:105)
24	head (1:5, 15:32) median and paired fins excluding caudal (6,7,10:14, 33:40, 59:69) caudal peduncle and fin (8,9, 41:58, 70:105)

To assess the fit of these modularity hypotheses, we used three approaches: (1) the relative strength of associations among subsets of landmarks compared to associations across these subsets, (2) correlations between shapes of subsets of landmarks, yielding a correlation matrix that can be used to test hypotheses of modularity, (3) and the goodness-of-fit of the covariance matrix derived from a model to the data.

3.4.6.2 *Covariation ratio*

We used the covariation ratio (CR) as a measure of the covariation between partitions (hypothesized modules) relative to the covariance within them. The CR was recently proposed by Adams (2016) and improves upon the widely used RV coefficient (Escoufier 1973; Klingenberg 2009, 2013) because it is unaffected by sample size or by the number of variables. If the modules are correctly delimited, the covariance between the two partitions should be lower than any other alternative partitioning because all of the alternatives will contain landmarks that covary. A null distribution of CR's is generated by randomly reassigning the landmarks and semi-landmarks into the same number of partitions as predicted by the hypothesis, with the additional constraint that each partition contains the same number of landmarks as in the hypothesis (Adams 2016). The CR value obtained for the hypotheses is then compared to the null distribution of CRs to assess statistical significance; the hypothesis of modularity is supported if its CR is lower than expected by chance (Adams 2016).

3.4.6.3 *Distance-matrix method*

The distance-matrix method, introduced by Monteiro et al. (2005), produces a correlation matrix between the shapes of subsets of landmarks. To obtain this matrix, the coordinates are partitioned into subsets corresponding to hypothesized modules, or parts of modules. In the present case, the coordinates are partitioned into head, dorsal fin, caudal fin, anal fin, paired fins, dorsal tail outline, and ventral tail outline. If each partition is superimposed after partitioning, the information about relative size and position within the body is removed from the data, leaving only information about shape. In this case, we did not perform superimposition after partitioning, so that the information about relative size and position would remain in the data. Pairwise Procrustes distances are calculated between all specimens (for each partition) and the matrix correlations between these pairwise distance matrices are then calculated,

yielding a correlation matrix that can be analyzed by conventional methods for studies of modularity.

Modularity was assessed using graphical modeling, which evaluates the goodness-of-fit of models predicting correlations between two modules, conditional on all variables (here, the partitions) in the data. The aim is to reconstruct the observed covariance using as few "edges" as possible, with edges between variables ("nodes") representing conditionally dependent traits (Whittaker 1990; Lauritzen 1996; Edwards 2000; Magwene 2001, 2009; Zelditch et al. 2009). The model is fit using maximum-likelihood. Because models differ in the number of fixed parameters, their relative fit can be assessed by the Akaike Information Criterion (AIC) (Akaike 1974).

3.4.6.4 *Minimum deviance method*

Instead of fitting models to a matrix of correlations between partitions, this method fits models to the covariance matrix of landmark coordinates. The fit of the hypotheses is assessed through the standardized gamma statistic (γ^*), a measure of the deviance between the model and the data (Richtsmeier et al. 2005; Márquez 2008). For the hypotheses, modules comprising subsets of landmarks are made statistically independent by placing them into orthogonal subspaces; intramodular covariances are estimated from the data (Márquez 2008). The null hypothesis is that the difference between the observed and expected covariance matrices is no greater than expected by chance; thus, a low *p*-value indicates that the model fits the data poorly (Parsons et al. 2012; Márquez 2014). The best fitting model is the one that deviates least from the data taking into account the number of fixed parameters. The γ^* is scaled as a function of the maximum γ value (calculated from a null model of no integration), and scaled a second time to account for the number of fixed parameters (Márquez 2008, 2014). This last step is performed by regressing the γ values on the number of fixed parameters, since both are linearly related (Márquez 2008, 2014). Although there is no method for

statistically comparing these γ* values, the strength of support for each hypothesis' ranking was assessed using a jackknifing procedure with 1000 replicates, removing 33% of species in each iteration.

3.4.7 Comparing evolutionary rates and disparity among partitions

In order to determine whether the rates of morphological evolution differed among partitions, we used the rate ratio (Denton and Adams 2015), which is a ratio between two multivariate rates (Adams 2014b). Rates are estimated for each high-dimensional complex and compared to each other by generating a null distribution of rate ratios that are obtained by simulating datasets along the phylogeny using a single rate model (Adams 2014b; Denton and Adams 2015). The default is that both complexes evolve under Brownian motion (Denton and Adams 2015).

3.4.8 Software

Landmarks and semi-landmarks were digitized with TPSDig2 (Rohlf 2013b) and superimposed using the package geomorph (Adams and Otarola-Castillo 2013) for R (R Core Team 2016). The correlation between tangent space and shape space was calculated using the package Morpho (Schlager 2016). Estimation of the parameters for the models of trait evolution were performed in a modified version of one of the functions of the package motmot (Thomas and Freckleton 2012). The updates to the function, which were kindly provided by Dr. Graham Slater, provide parameter estimates for the EB model which were not available in the original function, as well as AIC and AICc values for all of the models tested. For the analyses of modularity, the observed correlation matrices for the distance matrix-based method were generated using a script developed by Adam Rountrey [available as supplementary material of Zelditch et al. (2012), at http://booksite.elsevier.com/9780123869036/functions.php], and modified by M.L.Z. to account for phylogeny. Graphical modeling was performed

in MIM version 3.2.0.7 (Edwards 2000) and in R using the package ggm (Marchetti et al. 2014). The minimum deviance method was implemented using the program Mint version 1.61 (Márquez 2014). The covariance ratio and the rate ratio methods were both computed using the package geomorph (Adams and Otarola-Castillo 2013).

3.5 Results

3.5.1 Testing evolutionary models

The value that we obtained for Blomberg's K statistic is less than expected by a model of Brownian motion (K = 0.809, p = 0.001). This suggests that close relatives are less similar than expected under Brownian evolution (Blomberg et al. 2003). Such a result could indicate evolution towards a single stable adaptive peak (Blomberg et al. 2003; Revell et al. 2008), such as in an OU model of evolution. Given that different evolutionary processes can produce similar results in terms of phylogenetic signal (Revell et al. 2008), we used two additional approaches to investigate the underlying evolutionary process in our dataset: a model fitting approach and a disparity through time approach.

The results of model fitting also point towards an OU process. Based on their AIC rankings, the level of support for the OU model was better than for BM (ΔAIC = 85.37) and EB models (ΔAIC = 87.52). However, the estimated α parameter of the model was quite low (α = 0.007). We rescaled the phylogenetic tree using the estimated α parameter, and computed the evolutionary rate matrix. We then compared this evolutionary rate matrix to the covariation matrix of the original dataset using a Mantel test and obtained a strong correlation between the two matrices (r = 0.950, p = 0.001). This indicates that taking into account the OU model parameters changes very little to the structure of shape in our dataset. Using the rescaled phylogenetic tree, we also simulated trait evolution under the OU model and computed the resulting variance as

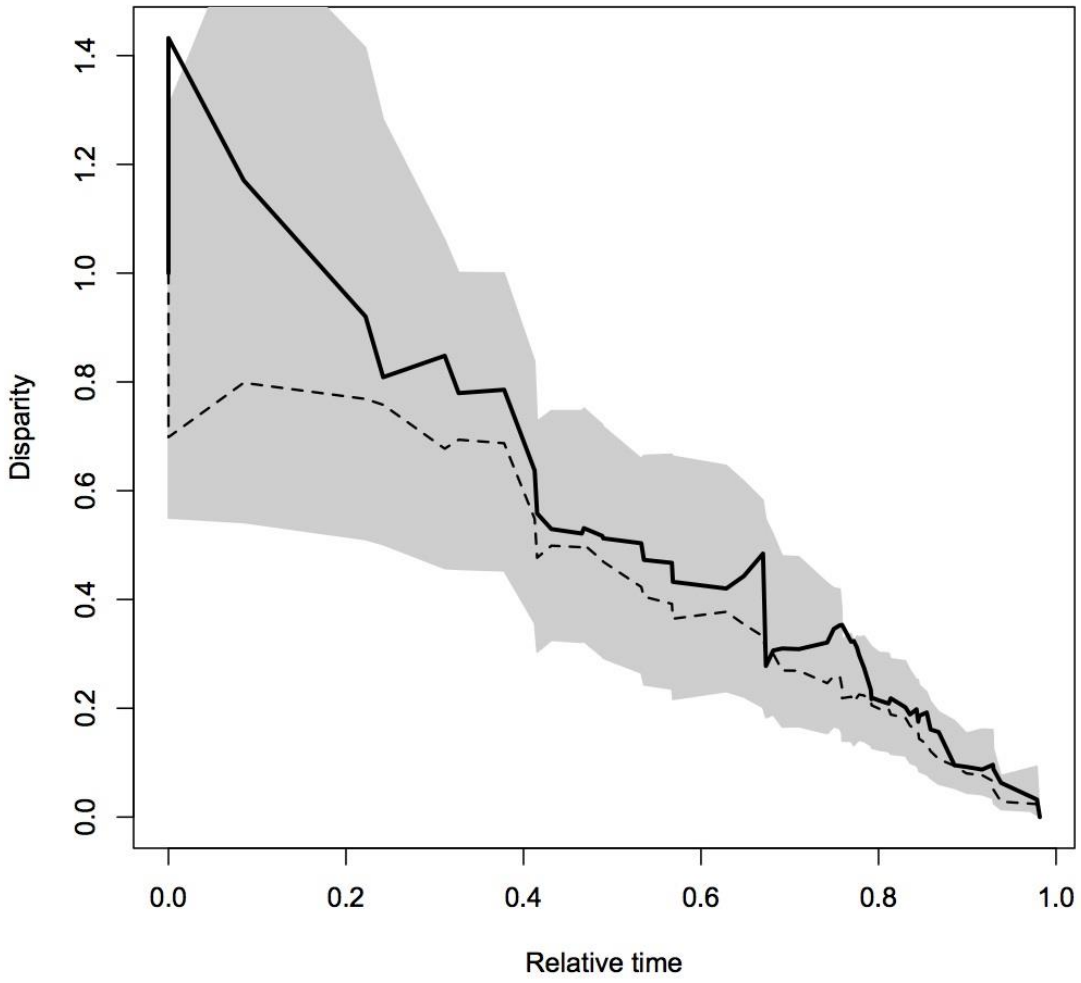

Figure 14: Disparity through time plot for our dataset of 58 actinopterygian species using a pruned version of the time-calibrated tree from Near et al. (2012) as the phylogenetic context for the analysis. The dashed line represents the results of simulations of shape evolution under Brownian motion, the grey-shaded area represents the 95% confidence interval, and the full line represents the observed data.

a measure of disparity. The ratio between the observed variance and the simulated variance was of 1.25, which implies that simulation of shape evolution under the OU model with these estimated parameters generates less disparity than what is actually observed.

As opposed to the model fitting approach, the results of the DTT analyses supported a BM model of character evolution (MDI = 0.129, $p = 0.112$; Figure 14). The discrepancy between methods could be suggestive that a more complex model of character evolution, for instance a model with multiple adaptive peaks, might be more appropriate. However, software has yet to be developed to accurately estimate parameters for these more complex models using multivariate datasets. Alternatively, OU might be favored because the methods are biased towards more complex models of character evolution, even when a simpler model offers a better fit.

Considering that the estimated α parameter was so low in the model fitting approach, and that a BM model was favored in the DTT analyses, we used a BM model of character evolution for subsequent analyses. Additionally, when we compared the evolutionary variance-covariance matrix to the non-phylogenetic covariance matrix, we obtained a very high correlation between the two matrices ($r = 0.908$, $p < 0.0001$). This indicates that both matrices are structurally very similar and that the phylogenetic component does not contribute much to the patterns of shape variation. Nonetheless, we used phylogenetic correction in most of our subsequent tests where taking into account phylogenetic signal was possible. However, given the level of similarity between the two matrices, we considered that analyses where a procedure currently does not exist to account for phylogeny could also be used (e.g., the minimum deviance method).

3.5.2 Covariance ratios

Twelve of the 24 hypotheses of modularity were supported as indicated by their statistically significant CRs (Table 16). These hypotheses had covariation ratios that ranged between 0.46 and 0.92. We also looked at the individual pairwise covariation ratios among partitions for each of the hypotheses and found that a single partition, the

Table 16 : Results of the statistical analyses of modularity using covariance ratios, graphical modeling and minimum deviance methods.

Hypothesis	Covariation ratio		Graphical modeling		Minimum deviance		
	CR	***p***	**Deviance**	**ΔAIC**	**γ***	***p***	**JK**
1	0.8674	0.005	67.11	40.01	-0.198	0.988	23%
2	1.0722	0.646	105.25	74.15	-0.186	0.77	31%
3	0.9605	0.135	56.68	29.58	-0.025	0.747	93%
4	0.9679	0.17	NA	NA	-0.263	0.999	71%
5	0.9063	0.017	70.03	34.93	-0.416	0.936	99%
6	0.9244	0.023	111.52	74.42	-0.207	0.614	53%
7	1.1199	0.74	66.41	31.31	-0.065	0.571	100%
8	0.9944	0.253	54.52	19.42	0.017	0.2	81%
9	0.8095	0.004	73.03	43.92	-0.192	0.947	27%
10	0.8192	0.001	114.90	73.80	-0.345	0.507	55%
11	0.8023	0.002	77.57	40.47	0.036	0.111	95%
12	0.9114	0.015	82.52	41.42	-0.282	0.45	68%
13	1.0924	0.873	70.63	29.53	-0.200	0.119	22%
14	0.9433	0.148	100.16	59.06	-0.173	0.095	66%
15	1.0435	0.411	123.21	80.11	-0.154	0.039	96%
16	1.1131	0.748	93.68	50.58	-0.180	0.066	45%
17	1.0982	0.804	115.43	70.33	-0.394	0.334	92%
18	0.9244	0.023	126.58	79.48	-0.292	0.041	70%
19	0.8804	0.003	135.50	86.40	-0.348	0.039	32%
20	0.4602	0.001	30.82	11.72	-0.249	1	77%
21	0.9614	0.139	50.89	23.79	-0.336	1	58%
22	0.9705	0.125	31.10	0	-0.376	1	47%

Hypothesis	Covariation ratio		Graphical modeling		Minimum deviance		
	CR	***p***	**Deviance**	**ΔAIC**	**γ***	***p***	**JK**
23	0.8268	0.01	26.17	7.07	-0.230	1	80%
24	0.8697	0.004	37.99	0.89	-0.375	0.92	55%

lower half of the tail outline excluding the base of the caudal fin, specific to hypothesis 19, has a relatively low CR with all other partitions ($0.17 < CR < 0.54$). We used phylogenetic partial least squares (PLS) to quantify the strength of the covariation between this partition and the others and found a high degree of integration between it and the other partitions, as quantified by the correlation between the scores on the first singular axes of these partitions ($0.56 < r\text{-}PLS < 0.87$).

3.5.3 Graphical modeling

Using graphical modeling, the best-fitting hypotheses are hypotheses 22, 24 ($\Delta AIC = 0.89$), 23 ($\Delta AIC = 7.07$) and 20 ($\Delta AIC = 11.72$). Hypotheses 22 and 24 are equally well supported: hypothesis 22 postulates that the tail (caudal fin + peduncle) forms one module, while the rest of the body forms a second module. Hypothesis 24 build on the former hypothesis by adding the head as a third module. Hypothesis 23 postulates that the head forms one module while the rest of the body forms a second module. Finally, hypothesis 20 postulates that the lower half of the caudal peduncle forms one module while everything else is integrated. All of these best supported hypotheses share one common characteristic: the dorsal, anal and paired fins are integrated. The differences among models stem mostly from what the head, tail and caudal fin are integrated with.

3.5.4 Minimum deviance method

The minimum deviance method, as currently implemented in Mint, does not take phylogeny into account. However, as mentioned previously, because the similarity is very high between the evolutionary variance-covariance matrix and the non-phylogenetic covariance matrix, we consider it unlikely that it would have a large effect on the results.

Contrary to the microevolutionary analysis from Larouche et al. (2015) where only three models had *p*-values close to one, only a few of the models in this macroevolutionary analysis have a *p*-value that is under the significance level. Ranking models by their standardized gamma values and jackknife support, the best fitting models are hypotheses 5 ($\gamma^* = -0.416$), 17 ($\gamma^* = -0.394$), 22 ($\gamma^* = -0.376$) and 24 ($\gamma^* = -0.375$), although the *p*-value for hypothesis 17 is relatively low ($p = 0{,}334$). Based on jackknife support, hypothesis 5 is the best supported in 99% of iterations, and hypothesis 17 is second best in 92% of iterations. Hypothesis 5 postulates that all of the fins form a single module, to the exclusion of the head and the caudal peduncle. Hypothesis 17 subdivides the fins module from hypothesis 5 into a paired fins module, a dorsal and anal fins module, and a caudal fin module while the head and caudal peduncle remain independent structures. The jackknife support for hypotheses 22 and 24 are far lower, respectively of 47% and 55%, consistent with the very slight difference in standardized gamma statistic of just 0.001 between them. Hypothesis 22 postulates that the tail (caudal fin + peduncle) forms one module, while the rest of the body forms a second module. Hypothesis 24 postulates that the head forms one module, the median and paired fins form a second module, and the tail forms a third module.

Table 17: Results of the evolutionary rate ratios method described in Denton and Adams (Denton and Adams 2015).

Hypothesis	Rate ratio		Hypothesis	Rate ratio	
	ratio	*p*		ratio	*p*
1	1.296	1	**13**	8.679	0.001
2	2.590	0.001	**14**	8.816	0.001
3	4.770	0.001	**15**	8.816	0.562
4	1.470	1	**16**	8.679	0.27
5	3.324	0.192	**17**	6.173	0.962
6	2.756	1	**18**	8.816	0.001
7	5.038	1	**19**	9.530	0.001
8	7.195	0.001	**20**	2.694	1
9	1.368	1	**21**	2.781	0.451
10	3.500	1	**22**	3.547	0.001
11	7.195	1	**23**	1.360	1
12	6.077	1	**24**	5.174	0.001

3.5.5 Evolutionary rate ratios

Ten of the 24 hypotheses of modularity were well supported based on their statistically significant rate ratios (Table 17). Of these, the highest rate ratios were obtained for hypothesis 19 (RR = 9.530), hypotheses 13 and 16 (RR = 8.679), and hypotheses 14, 15 and 18 (RR = 8.816). The fact that some hypotheses have identical rate ratios reflects that these modularity hypotheses share some partitions that are found to have both the highest and the lowest evolutionary rates. Not all hypotheses that yield significant rate ratios are well-supported hypotheses of modularity. The modularity hypotheses that are well supported by both the CR ratio and the rate ratio methods are hypotheses 18, 19 and 24. Using graphical modeling, of the five best-supported hypotheses based on their

AIC values, only the two best fitting models, hypotheses 22 and 24, have significant evolutionary rate ratios. Hypotheses 22 and 24 are respectively the third and fourth best-fitting hypotheses based on their standardized γ values, while the first and second best-fitting hypotheses using this method were not found to be significant by the rate ratio method.

3.5.6 Comparing micro- and macroevolutionary patterns of integration

We compared the evolutionary rate matrix from the macroevolutionary dataset to the covariance matrices of both intraspecific datasets used in Larouche et al. (2015). The structure of the evolutionary variance-covariance matrices differs from the covariance matrices of both *D. rerio* (r = 0.131, $p = 0.224$) and *C. eos* (r = 0.131, $p = 0.214$). The covariance matrices for *D. rerio* and *C. eos* are however structurally nearly identical (r = 1, $p < 0.0001$).

Hypotheses 20 through 24 had not been tested using the microevolutionary datasets. Upon analyzing these novel hypotheses of morphological integration using the *D. rerio* and *C. eos* datasets (see Annexe F), we found that some of these hypotheses are also well supported. For the *D. rerio* dataset, the best supported modularity hypotheses are respectively hypotheses 20, 1, 9 and 23, while for the *C. eos* dataset, these are hypotheses 23, 20, 1 and 9. Thus, for the two microevolutionary datasets the best supported hypotheses are identical, although they are ordered differently based on their AIC rankings (Figure 15).

Using the minimum deviance method, the four best supported modularity hypotheses for the macroevolutionary dataset are respectively hypotheses 5, 17, 22 and 24. Comparatively, for the *D. rerio* dataset, the best supported modularity hypotheses are respectively hypotheses 9, 4, 1, 23 and 20 while for the *C. eos* dataset, these are hypotheses 23, 9, 4, 1 and 20. Additionally, for *D. rerio* and *C. eos*, these hypotheses

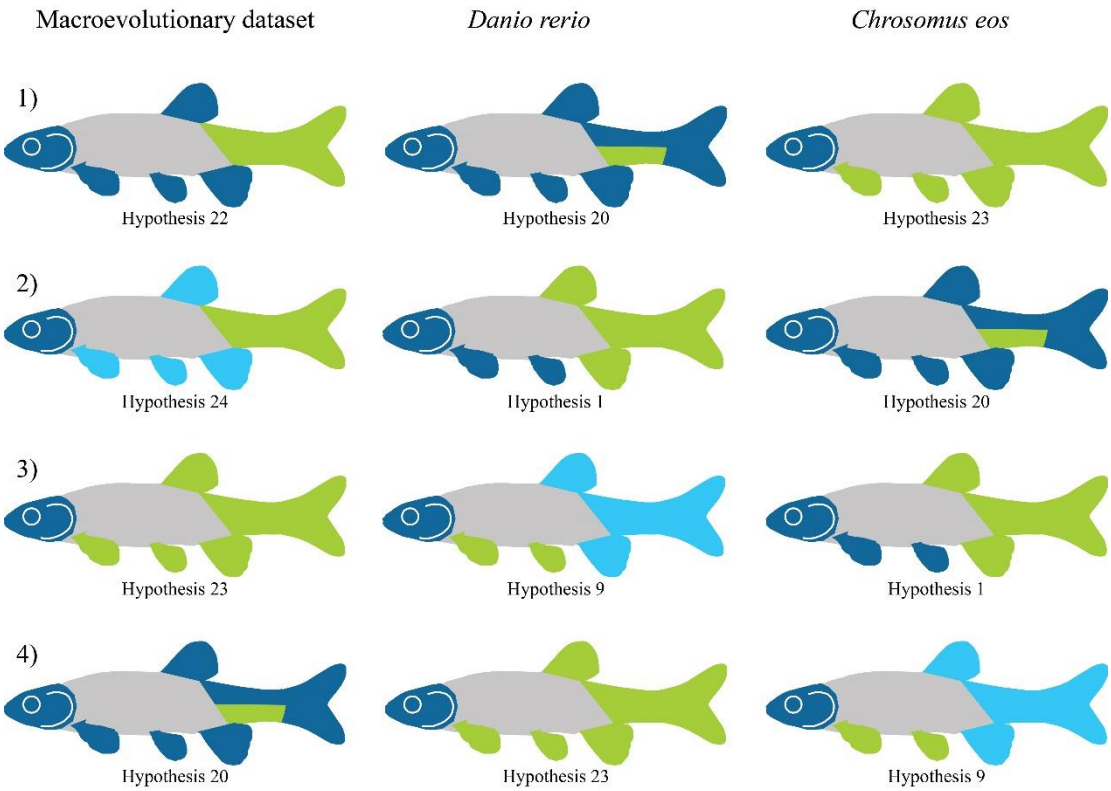

Figure 15: Graphical representations of the four best-supported modularity hypotheses (rows) for the macroevolutionary, zebrafish (*Danio rerio*) and Northern redbelly dace (*Chrosomus eos*) datasets (columns), based on their AIC rankings using graphical modeling. Regions of the body sharing the same coloration pattern form putative evolutionary (macroevolutionary dataset) or variational (*D. rerio* and *C. eos* datasets) modules.

are the only ones with p-values close to 1, whereas for the macroevolutionary dataset, most hypotheses fit well based on their *p*-values. Again the microevolutionary datasets converge to the same best-fitting models although in a different order based on their rankings by standardized gamma values. However in this case, there is no overlap between the four best models when comparing the micro- and the macroevolutionary datasets (Figure 16).

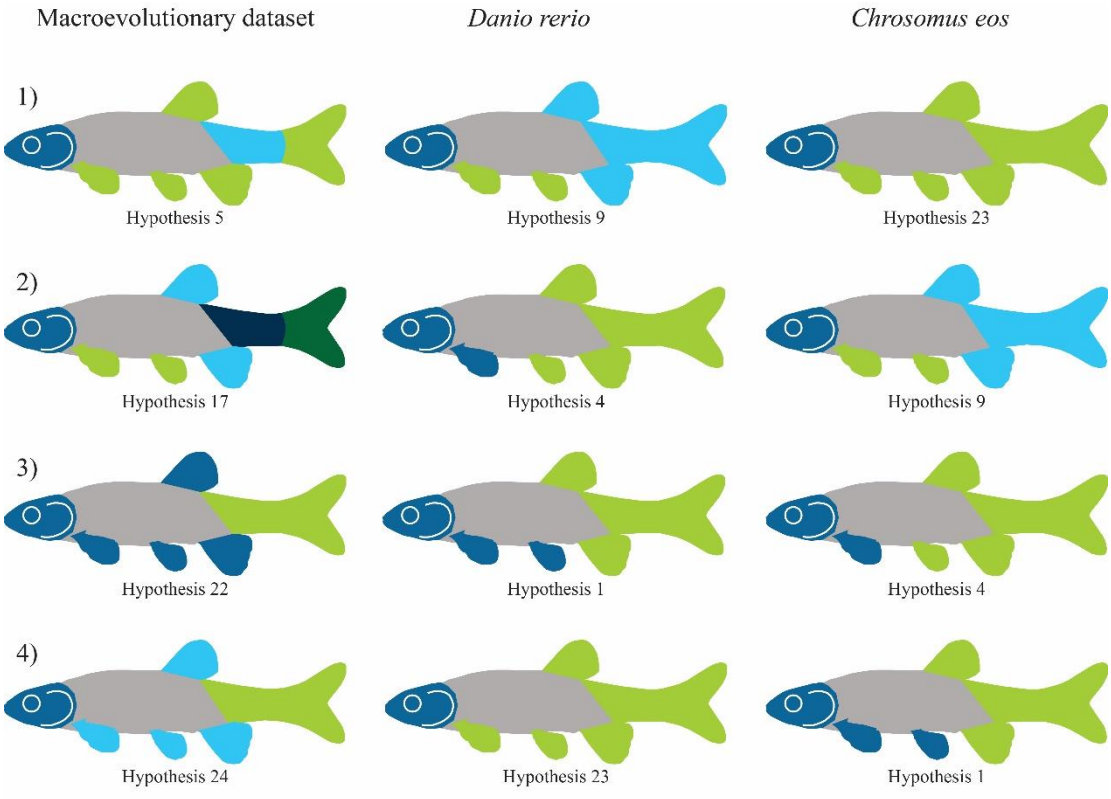

Figure 16: Graphical representations of the four best-supported modularity hypotheses (rows) for the macroevolutionary, zebrafish (*Danio rerio*) and Northern redbelly dace (*Chrosomus eos*) datasets (columns), based on their standardized γ values using the minimum deviance method. Regions of the body sharing the same coloration pattern form putative evolutionary (macroevolutionary dataset) or variational (*D. rerio* and *C. eos* datasets) modules.

3.6 Discussion

Our analyses asked two important questions: (1) do partitions identified as putative evolutionary modules differ in rates of morphological evolution and (2) do patterns of morphological integration and modularity at the microevolutionary scale translate to patterns of evolutionary integration and modularity at the macroevolutionary scale? The answer to the first of these questions is that a large difference in rates exists among

partitions predicted by one of the best fitting hypotheses of modularity across methods, a hypothesis that predicts three modules: head, trunk and tail. The answer to the second question is that variational and evolutionary modularity share some similarities in overall covariance structure and patterns of integration. This is exemplified by the results of graphical modeling where some of the best supported hypotheses of modularity are common to both the micro- and the macroevolutionary datasets.

3.6.1 Support for evolutionary fin modules

The best-supported patterns of morphological integration and modularity differ across methods, consistent with our previous results for variational modularity (Larouche et al. 2015). These discrepancies presumably arise from conceptual distinctions among the methods. More precisely, the methods differ in terms of the concept of modularity that is tested. The graphical modeling approach and the minimum deviance method both emphasize quasi-independence among modules, which is an important prerequisite for evolvability (Hansen 2003; Hansen et al. 2003; Hansen 2006). Another important difference is more methodological: not all methods allow for statistically comparing hypotheses or even ranking them. Results of graphical modeling can be ranked based on their AIC values and results of the minimum deviance method can be ranked based on their standardized gamma statistic and jackknife support, as opposed to the CR which does not allow for ranking models. For these reasons, more emphasis is placed on the results from graphical modeling of the correlations between the distributions of shape, and the minimum deviance method.

Focusing on the macroevolutionary dataset, among all of the hypotheses tested, hypothesis 24 is well supported across all of the methods that we used. Hypothesis 24 postulates that the head forms one evolutionary module, the fins along the trunk form a second evolutionary module and the tail and caudal fin form a third evolutionary module. Hypothesis 22 is also well supported across all methods used, excepting the

CR ratio. Hypothesis 22 differs from hypothesis 24 in that the head is integrated with the fins inserted along the trunk. In our previous analysis focusing on patterns of integration in two cyprinid species, we had reported that the paired fins were well supported as forming one variational module, while the tail, the dorsal and the anal fins formed a second variational module (Larouche et al. 2015). Integration of the posterior trunk and tail region had been interpreted as resulting from functional requirements of a subcaranguiform mode of locomotion (Webb 1975; Lindsey 1978; Sfakiotakis et al. 1999). The results of the macroevolutionary analysis of modularity are also suggestive of a pattern of modularity based on functional integration: following hypothesis 24, the head is functionally integrated for breathing and feeding, while the tail and caudal fin are functionally integrated for a caudal fin-based propulsion. In this case however, the dorsal and anal fins are not incorporated into a posterior trunk and tail evolutionary module, contrary to the microevolutionary analysis of modularity. This could reflect the fact that in this broader taxonomic sample, the fish species considered do not all use subcaranguiform locomotion, as opposed to *D. rerio* (Plaut and Gordon 1994) and *C. eos* (T. Grünbaum, pers. comm.). The sample includes many acanthopterygian fishes that use a variety of types of propulsion, including some fishes that rely more on the paired fins for locomotion. Perhaps this also explains why at the macroevolutionary scale, the paired fins are instead integrated with the dorsal and anal fins. This integration pattern could reflect coordinated shifts in paired and median fins configurations to accommodate changes in locomotion and/or foraging modes (Webb 1982, 1984; Lauder and Drucker 2004).

3.6.2 Modularity, morphological disparity and rates of morphological evolution

Modularity has been hypothesized to influence rates of morphological evolution (Wagner 1996). For instance in a study focusing on mantis shrimp raptorial appendages, Claverie and Patek (2013) found that groups characterized by higher modularity also displayed higher rates of phenotypic evolution. Another hypothesis is

that modularity might influence the mode of evolution rather than its tempo. One such hypothesis is that a modular organization might influence disparity by facilitating shifts in the timing of developmental events (Goswami et al. 2009; Sears 2014). Yet another hypothesis is that modularity can constrain morphological evolution and contribute to overall lower rates of morphological evolution (Aguilar-Medrano et al. 2016). Reflecting this, Goswami and Polly (2010) found some support for the hypothesis that the strong morphological integration of some cranial modules constrains morphological variation. Goswami et al. (2014) also found that modules with lower overall integration were generally more disparate than modules with strong overall integration. Additionally, Goswami et al. (2014) observed that although there was a relationship between disparity and strength of integration in elements of the mammalian cranium, they did not find a relationship between high disparity and higher rates of morphological evolution, or between integration and rates or morphological evolution. Brusatte et al. (2011) also highlighted a discrepancy between disparity and evolutionary rates in archosaurian evolution.

Focusing on the differences in evolutionary rates among the best supported hypotheses of modularity from the graphical modeling and the minimum deviance methods, hypotheses 5, 17, 20 and 23 did not yield significant results in terms of the rates ratio. Contrastingly, hypotheses 22 and 24 yielded highly significant rate ratios. Hypothesis 22 is a two module hypothesis where the head and the fins along the trunk form one module, while the tail and caudal fin form a second module. Hypothesis 24 is a three module hypothesis where the head and the trunk region each forms their own evolutionary modules. Hypothesis 24 has a higher evolutionary rate ratio than hypothesis 22. Furthermore, the three module model from hypothesis 24 showed that the trunk section had a rate of morphological evolution which was significantly higher than the head and the tail sections. In a study focusing on lantern fishes (Myctophiformes), Denton and Adams (2015) found that the rate of morphological evolution of the trunk region was higher compared to the rate of morphological

evolution of the head and tail combined as a single partition. Because they expected the head region to have higher rates of morphological evolution, Denton and Adams (2015) hypothesized that the higher rates of morphological evolution of the trunk region when compared to the head could be explained in part by the similarity in diet among species belonging to the clade analyzed. The fact that we also obtain higher rates of morphological evolution for the trunk with a phylogenetically much broader sample suggests that another explanation can be considered. Because in our dataset, the landmarks of the trunk region are all fin insertion points, these higher rates of morphological evolution could reflect the evolutionary trend among actinopterygians for shifts in the size and relative position of both median and paired fins (Webb 1982; Lauder and Liem 1983; Lauder and Drucker 2004). Thus, these higher rates of morphological evolution may contribute to the extensive disparity in fin configurations seen in actinopterygians.

To test this hypothesis that higher rates of morphological evolution favors the disparification in fin configurations, we quantified and compared the disparity among the three partitions of hypothesis 24. We found that the morphological disparity in the trunk region was an order of magnitude larger than that of both the head and the tail regions. The increased disparity in the trunk region combined to the higher rates of morphological evolution are concurrent with the idea that modularity can promote morphological disparity by allowing differing rates of morphological evolution among partitions.

3.6.3 Correspondence between micro- and macroevolutionary patterns of integration

The structural comparison between the covariation matrices generated for *D. rerio* and *C. eos* resulted in a correlation of one. This suggests that patterns of morphological integration are conserved between these two cyprinid species. The comparison between

each of the interspecific covariance matrices and the evolutionary variance-covariance matrix for the macroevolutionary dataset indicate however that the evolutionary rate matrix is structurally different. Additionally, among the methods used to assess the fit of modularity hypotheses, the best supported hypotheses are generally the same for *D. rerio* and *C. eos*. Using the minimum deviance method, the best supported models differ between the microevolutionary and macroevolutionary dataset, whereas using graphical modeling, hypotheses 20 and 23 are well supported for both micro- and macroevolutionary datasets. The latter result suggests that despite differences in landmarks covariation structure across evolutionary scales, some similarities remain in terms of patterns of morphological integration and modularity. This provides some evidence that variational modules can be a target for natural selection, which can lead to evolutionary modularity.

Similarities between intra- and interspecific patterns of integration and modularity are not uncommon and have been observed in a diverse array of organisms and structures. The mammalian cranium has often been used as a model structure for studies on morphological integration and modularity. Similarities in patterns of cranial integration have been reported among species in comparisons across various taxonomic levels (Cheverud 1996b; Marroig and Cheverud 2001; Goswami 2006; Marroig et al. 2009; Porto et al. 2009; Goswami et al. 2014). Although general similarities exist in integration patterns among taxa, there are also differences which Marroig and Cheverud (2001) interpreted as meaning that patterns of cranial integration are likely to evolve. For instance, patterns of integration of the cranium are generally found to be similar across therian mammals (Goswami 2006; Marroig et al. 2009; Porto et al. 2009), yet Goswami (2006) found that these differed markedly from those of monotremes. Goswami et al. (2014) further suggested that patterns of both morphological integration (within species) and evolutionary integration tend to be conserved in the mammalian cranium, although differences exist between monotremes, marsupials and placentals. Porto et al. (2009) also observed that, although a single

hypothesis of modularity for the cranium was best supported across metatherians, some orders of eutherians deviated from the best supported eutherian modularity hypothesis. Additionally, despite strong similarities in cranial integration patterns across mammals, the overall level of integration differs between metatherians and eutherians, which is suggestive of a greater modularization of the cranium in the more derived eutherians when compared to metatherians and most of the more basal eutherians (Marroig et al. 2009; Porto et al. 2009). Notwithstanding these results, the support for highly similar cranial integration patterns across members of an evolving lineage are not always supported. For instance, based on differences in the best supported models of integration and modularity across *Anolis* lizard species, Sanger et al. (2012) suggested that the conserved cranial integration patterns among mammals might represent an exception rather than a rule.

Similarities in integration patterns have also been observed in morphological structures other than the cranium. Young and Hallgrímsson (2005) found that patterns of limb integration were similarly structured across mammalian species, but that shifts in covariation structure could occur, for instance to allow for greater functional specialization. Sears et al. (2013) found that in both marsupials and placentals, patterns of morphological integration of the shoulder girdle could be conserved across micro- and macroevolutionary scales. Additionally, in accordance with Goswami (2006) and Goswami et al. (2014)'s conclusions, these authors observed marked differences in patterns of integration between marsupials and placentals (Sears et al. 2013). All of these observations suggest that although patterns of integration and modularity tend to be conserved over large phylogenetic scales, these patterns can also be relaxed during the evolutionary history of some subclades, possibly in relation to shifts in functional requirements.

Perhaps in the present case, the differences between the micro- and the macroevolutionary datasets in terms of patterns of integration and modularity can be in

part explained by the large difference in taxonomic scale between the datasets. The zebrafish (*D. rerio*) and Northern redbelly dace (*C. eos*) are both cyprinids (Cyprinidae; Cypriniformes), which are members of the Ostariophysi, a large clade of predominantly freshwater fishes. Although our macroevolutionary dataset contained six representatives of the ostariophysans, it also contained 30 representatives of the acanthopterygians. Acanthopterygians are extremely diversified (14 797 species; Nelson et al. 2016) and are characterized by substantial changes in the morphology and relative positioning of median and paired fins. The differences between the macroevolutionary patterns of integration and those of the two cyprinid species could reflect that the former is a composite of patterns inherent to a number of actinopterygian lineages. From a conceptual point of view, Hallgrímsson et al. (2009) proposed that there could be a lack of correspondence between developmental and variational modules because patterns of variational modularity result from several partially overlapping developmental processes. This considered, it would not be surprising that a similar palimpsest exists between variational and evolutionary patterns of morphological integration.

3.7 Conclusion

Our results suggest that patterns of evolutionary covariation may be driven in part by patterns of variational modularity and integration at a microevolutionary scale, yet that there are also differences that are likely brought about by shifts in patterns of integration among some lineages. Focusing on the results of methods that emphasize quasi-independence, the best-fitting models commonly show that the trunk region is integrated, and that the tail region is also integrated. Among these best supported hypotheses of modularity, the head region can be integrated with the trunk region, or it can form its own evolutionary module. Additionally, the trunk region, which includes the insertion points of all median and paired fins, excepting the caudal fin, is characterized by a significantly higher rate of phenotypic evolution. This provides

evidence that modularity can promote morphological disparification by allowing different rates of phenotypic evolution among modules. The combination of these methods provides a holistic view combining information on trait covariation as well as information on the macroevolutionary consequences of a modular organization in biological systems.

CONCLUSION GÉNÉRALE

Contexte, originalité de l'étude et rappel des objectifs

Le travail de recherche effectué dans le cadre de cette thèse doctorale est fortement intégrateur puisqu'il relie des aspects observables dans la diversité du vivant, soit la disparité morphologique entre les taxons, avec les mécanismes sous-jacents qui peuvent favoriser l'émergence de cette disparité, le tout dans un contexte phylogénétique. Cette thèse doctorale comportait trois objectifs importants. Le premier était d'analyser les patrons macroévolutifs de disparité morphologique en termes de présence/absence des nageoires, ainsi que d'analyser les patrons de covariation dans ces données dans le but d'identifier des modules basés sur la coordination dans la perte ou dans l'ajout de nageoires. Le deuxième objectif était d'analyser et de comparer les patrons de covariation dans la position relative des nageoires à l'échelle microévolutive dans le but d'identifier des modules variationnels. Le troisième objectif était quant à lui d'analyser ces mêmes patrons de covariation dans la position relative des nageoires, mais cette fois à l'échelle macroévolutive, dans le but d'identifier des modules évolutifs. La majorité des études s'intéressent soit à la modularité développementale, soit à la modularité variationnelle, soit à la modularité évolutive, mais les études qui font le lien entre même seulement deux de ces trois niveaux d'organisation sont plus rares (p. ex. Klingenberg et al. 2001; Monteiro et al. 2005; Allen 2008; Hallgrímsson et al. 2009; Sears et al. 2013; Goswami et al. 2014). Les résultats obtenus pour les trois chapitres de cette thèse intègrent donc des processus fondamentaux qui se produisent à différentes échelles du vivant, soit à l'échelle de l'individu, à celle des populations ainsi qu'à l'échelle macroévolutive.

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Principaux résultats

Parmi les conclusions du premier objectif, la production d'un super-arbre phylogénétique a permis de consolider les résultats d'un grand nombre d'analyses phylogénétiques publiées depuis l'avènement des méthodes phylogénétiques modernes. La majorité des phylogénies publiées jusqu'à présent focalisaient sur l'une ou l'autre des lignées évolutives majeures de poissons. Le présent super-arbre a donc permis de mettre en parallèle l'ensemble de ces résultats selon une approche consensuelle.

Deuxièmement, la superposition des caractères de nageoires sur le super-arbre des poissons permet de mettre en évidence que la disparité morphologique n'est pas répartie uniformément au sein des groupes de poissons. Les agnathes, les chondrichthyens ainsi que les actinoptérygiens dérivés sont nettement plus diversifiés en termes de configurations des nageoires. La disparité morphologique au sein des agnathes résulte surtout de différences entre les taxons quant à la présence ou l'absence des différentes nageoires médianes et paires alors que celles-ci apparaissent séquentiellement au cours de l'histoire évolutive de ces poissons basaux, générant graduellement de nouvelles combinaisons en fonction des groupes. Cela représente donc une exploration de l'espace morphologique où diverses combinaisons de présence et de nombre de nageoires sont adoptées. La disparité morphologique dans les configurations de nageoires chez les chondrichthyens est surtout associée à une réduction du nombre de nageoires médianes présentes dans certains groupes. Ceci relève surtout des batoïdes (raies et poissons-scies) qui, sur une base fonctionnelle, utilisent les nageoires paires comme principal moyen de locomotion et deviennent donc moins dépendants des nageoires médianes (Rosenberger 2001; Schaefer and Summers 2005; Franklin et al. 2014). Quant aux nageoires pectorales et pelviennes, elles ne sont que très rarement perdues chez les chondrichthyens: les ptérygopodes, qui constituent une modification d'une partie des nageoires pelviennes chez les mâles sont d'ailleurs

considérés comme étant une synapomorphie du groupe (Schaeffer and Williams 1977; Maisey 1986; Grogan et al. 2012). Finalement, chez les actinoptérygiens, les patrons de disparité morphologique relèvent à la fois de la perte de certaines, parfois même de toutes les nageoires, mais également de l'addition de nouvelles nageoires. Ces additions résultent soit de la duplication de nageoires préexistantes comme chez la morue et ses trois nageoires dorsales, soit de l'addition de nageoires qui correspondent à des nouveautés évolutives, telle que la nageoire adipeuse.

Troisièmement, la superposition des données de présence/absence a également permis de considérer des scénarios d'apparition séquentielle des appendices locomoteurs chez les poissons. À la lumière de la répartition des caractères dans la phylogénie, une hypothèse qui semble raisonnable serait que les nageoires paires, tout comme les nageoires impaires, sont apparues d'abord sous la forme d'appendices allongés au sein des agnathes, avant d'être éventuellement modifiées en nageoires plus circonscrites dans leur étendue, et de ce fait plus mobiles (Zug 1979; Coates 1993; Tabin and Laufer 1993; Tamura et al. 2001; Yonei-Tamura et al. 2008).

Finalement, une autre conclusion importante de ce premier objectif est que certaines nageoires présentent une forte covariation en termes de leurs données de présence/absence, notamment les nageoires dorsales et anales, et les nageoires pectorales et pelviennes. La coordination dans les états de caractère de ces paires de nageoires suggère que celles-ci pourraient former des modules à l'échelle macroévolutive.

Les résultats du second objectif ont permis de mettre en évidence qu'à l'échelle microévolutive, certaines parties du corps du poisson-zèbre (*Danio rerio*) et du ventre rouge du Nord (*Chrosomus eos*) forment des modules variationnels. Plus précisément, la majorité des hypothèses les plus fortement supportées suggèrent que les nageoires dorsale, anale et caudale forment un module variationnel qui inclut aussi le pédoncule

caudal. Les hypothèses voulant que les nageoires pectorales et pelviennes forment un second module variationnel, et que la région de la tête forme un troisième module variationnel sont également bien supportées, quoiqu'à moins fort titre que le module de la région postérieure du tronc et de la queue. D'un point de vue fonctionnel, il n'est pas surprenant que la région postérieure de ces deux espèces de cyprinidés forme un module variationnel. En effet, le poisson-zèbre (Plaut and Gordon 1994) et le ventre rouge du Nord (T. Grünbaum, comm. pers.) utilisent tous deux un mode de locomotion appelé subcaranguiforme. Ce mode de locomotion implique des ondulations de la partie postérieure du tronc et de la queue qui sont éventuellement transmises à la nageoire caudale en tant que principal moyen de propulsion (Webb 1975; Lindsey 1978; Sfakiotakis et al. 1999). Ainsi, l'intégration morphologique dans cette région du corps pourrait dépendre davantage de contraintes fonctionnelles liées à la locomotion, plutôt que de l'action des modules développementaux sous-jacents.

De plus, il a été constaté que les méthodes utilisées pour tester les hypothèses de modularité ne convergent pas toutes sur les mêmes résultats. Malgré cela, chacune des méthodes produit des résultats concordants entre *D. rerio* et *C. eos*. Ceci suggère que les patrons d'intégration morphologique font l'objet d'un certain conservatisme phylogénétique, tout au moins à l'échelle de la famille dans ce cas-ci. Ce conservatisme phylogénétique des patrons d'intégration morphologique et de modularité est aussi appuyé par le fait que les modules variationnels identifiés pour ces deux espèces de cyprinidés correspondent bien avec les modules identifiés dans le cadre du premier objectif de cette étude, malgré le fait que la nature des données à l'origine de ces conclusions soit très différente.

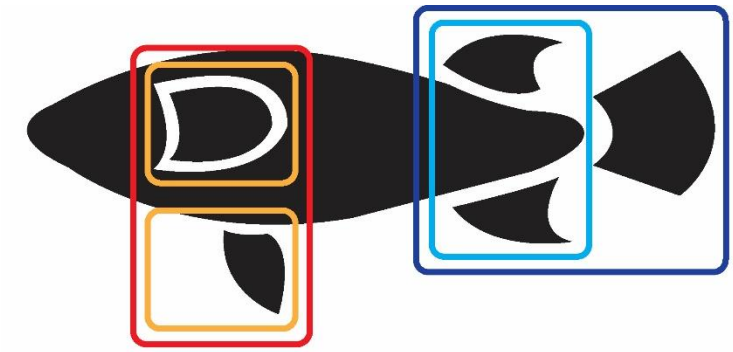
Quant au troisième objectif, l'une des hypothèses de modularité évolutive les mieux supportées au sein des diverses méthodes employées suggère que le corps du poisson peut être subdivisé en trois régions intégrées qui correspondraient donc à des modules évolutifs : la tête, le tronc, et la queue incluant la nageoire caudale. De surcroît, la

région du tronc, représentée principalement par les points d'insertion des nageoires médianes et paires, possède un taux d'évolution morphologique significativement plus rapide en plus d'être morphologiquement bien plus disparate que les régions de la tête et de la queue. Il est bien connu que des changements au niveau de l'organisation des appendices locomoteurs sont une tendance évolutive majeure au sein des actinoptérygiens (Webb 1982, 1984; Lauder and Drucker 2004). Ces résultats corroborent l'hypothèse selon laquelle des changements dans les taux d'évolution entre des modules peuvent influencer l'accumulation de disparité morphologique au sein d'un clade.

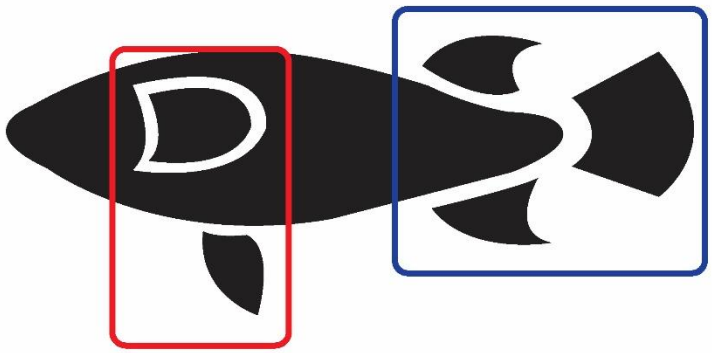
De plus, du fait que certaines des hypothèses de modularité les mieux supportées pour l'analyse macroévolutive le sont aussi pour *D. rerio* et *C. eos*, cela suggère que les patrons d'intégration morphologique à l'échelle microévolutive peuvent être en partie responsables des patrons d'intégration morphologique et de modularité à l'échelle macroévolutive. La correspondance n'est cependant pas parfaite, ce qui résulte probablement du fait que les patrons d'intégration morphologique observés à si large échelle phylogénétique représentent un amalgame des patrons propres à plusieurs lignées évolutives d'actinoptérygiens. Cela rappelle le modèle du palimpseste proposé par Hallgrìmmson et al. (2009) afin d'expliquer pourquoi les patrons d'intégration morphologique observés ne correspondent pas toujours aux attentes basées sur ce qui est connu de leurs déterminants développementaux. Selon ce modèle, l'origine de ces différences est que plusieurs processus développementaux participent aux patrons de covariation observés, et que ces processus n'ont pas tous les mêmes délimitations spatiales ou temporelles au cours de l'ontogenèse (Hallgrímsson et al. 2009). Une correspondance absolue entre les modules développementaux et variationnels ne devrait donc pas toujours être attendue puisque les modules variationnels résultent de l'action combinée d'une série de processus développementaux dont les effets peuvent se chevaucher et/ou s'annuler entre eux (Hallgrímsson et al. 2009). La concordance imparfaite entre les patrons d'intégration morphologique observés à l'échelle

macroévolutive et ceux des deux espèces de cyprins résulterait donc d'une situation analogue : les modules évolutifs identifiés ici à l'échelle des actinoptérygiens représenteraient un mélange des patrons d'intégration morphologique et de modularité propres à plusieurs lignées évolutives qui composent ce clade.

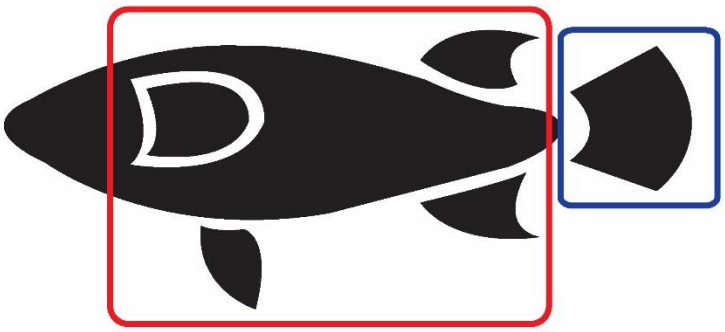
Un objectif important de ce travail doctoral était d'évaluer par différentes méthodes des hypothèses de modularité ayant trait à l'organisation des nageoires chez les poissons. La figure 17 présente une synthèse des modules de nageoires les mieux supportés dans chacun des chapitres de cette thèse. Il est intéressant de constater que les modules variationnels suggérés dans le second chapitre ressemblent davantage aux modules évolutifs suggérés dans le premier chapitre qu'aux modules évolutifs suggérés dans le troisième chapitre. Ceci peut paraître surprenant considérant les différences importantes quant à la nature des données et quant aux analyses utilisées entre le premier chapitre et les deux suivants. L'échantillonnage de taxons du Chapitre 3 incorpore cependant une proportion importante d'acanthoptérygiens, un groupe au sein duquel des changements dans la configuration des nageoires paires et médianes représentent une tendance évolutive majeure. Comparativement, une proportion importante des ordres échantillonnés dans le premier chapitre sont des actinoptérygiens basaux qui présentent tous des patrons de configuration des nageoires très similaires. Il existe néanmoins aussi des similitudes entre les patrons d'intégration morphologique et de modularité suggérés par chacun des trois chapitres de cette thèse. Ainsi, dans tous les cas les nageoires pectorales et pelviennes tendent à être intégrées, tout comme les nageoires dorsale et anale. Cette observation est congruente avec l'hypothèse que ces paires de nageoires forment des modules. Conséquemment, ces deux paires de nageoires (pectorales/pelviennes et dorsale/anale) pourraient tendre à demeurer intégrées l'une à l'autre tout en entretenant des liens plus flexibles avec les autres structures environnantes. Ceci permettrait d'expliquer les différences dans les patrons d'intégration morphologique et de modularité observés entre les trois chapitres.



Modules évolutifs basés sur les résultats du Chapitre 1



Modules variationnels basés sur les résultats du Chapitre 2



Modules évolutifs basés sur les résultats du Chapitre 3

Figure 17 : Résumé des hypothèses de modularité des nageoires les mieux supportées pour chacun des chapitres de cette thèse doctorale.

Portée de l'étude

Le super-arbre produit dans le cadre de cette thèse doctorale représente à lui seul un résultat majeur puisqu'il constitue la première synthèse de l'information phylogénétique concernant autant d'ordres de poissons en utilisant des méthodes phylogénétiques modernes. La majorité des analyses récentes focalisent sur certains groupes particuliers, notamment les interrelations au sein des agnathes (p. ex. Forey 1995; Janvier 1996a; Donoghue et al. 2000; Donoghue and Smith 2001; Sansom et al. 2010; Turner et al. 2010; Keating and Donoghue 2016), des gnathostomes basaux (p. ex. Brazeau 2009; Davis et al. 2012; Zhu et al. 2013; Dupret et al. 2014; Giles et al. 2015c; Long et al. 2015; Burrow et al. 2016; Qiao et al. 2016) ou des actinoptérygiens dérivés (p. ex. Miya et al. 2003; Springer and Orrell 2004; Miya et al. 2005; Kawahara et al. 2008; Setiamarga et al. 2008; Miya et al. 2013; Near et al. 2013; Eytan et al. 2015). La topologie obtenue pour le super-arbre suggère ente autres ques les cyclostomes, les placodermes et les acanthodiens sont des groupes paraphylétiques, et que les placodermes sont des gnathostomes basaux alors que les acanthodiens sont des chondrichthyens basaux.

L'apparition séquentielle des appendices locomoteurs est également une question qui a suscité beaucoup d'intérêt dans le domaine de la biologie évolutive au cours des dernières décennies, notamment en ce qui concerne l'évolution des membres pairs (Coates 1993; Tabin and Laufer 1993; Coates 1994; Shubin et al. 1997; Coates and Cohn 1999; Coates 2003; Yano and Tamura 2013). Chez les poissons, l'organisation des nageoires est associée à des caractéristiques écologiques telles que l'utilisation de l'habitat, le mode d'alimentation et le type de locomotion (Webb 1975; Lindsey 1978; Webb 1982, 1984; Sfakiotakis et al. 1999; Shubin and Davis 2004) pour n'en citer que quelques-unes. De plus, quoique des hypothèses de modularité aient déjà été proposées en ce qui concerne l'apparition de certaines des nageoires (p. ex. nageoire adipeuse, nageoire dorsale épineuse des acanthoptérygiens), les résultats de cette thèse

fournissent un cadre plus global dans lequel l'apparition séquentielle de l'ensemble des nageoires est considérée selon une perspective de modularité.

Les résultats de cette étude suggèrent qu'il existe une relation entre l'organisation modulaire des systèmes biologiques et la disparité morphologique qui peut s'accumuler au sein d'un groupe taxonomique. En effet, une conclusion importante de ce travail doctoral est que les modules peuvent différer les uns des autres en termes de taux d'évolution et de disparité morphologique. Quoique les poissons aient été utilisés comme organismes modèles, les résultats et les conclusions de l'étude ont une portée qui dépasse largement le contexte taxonomique de ces vertébrés basaux. L'émergence des nageoires paires revêt une importance toute particulière considérant qu'il est bien établit que celles-ci sont les précurseurs des membres pairs chez les tétrapodes. Les connaissances en termes de mécanismes évolutifs concernant l'apparition et la diversification des nageoires paires acquises dans le cadre de cette thèse peuvent donc être étendues à l'étude de la diversification des membres pairs chez les tétrapodes. Les membres pairs des tétrapodes fournissent un exemple classique de modularité en tant que moteur de disparité : la quasi-indépendance entre les membres antérieurs et postérieurs est considérée comme un prérequis important pour l'émergence de certaines structures spécialisées, telles que les ailes des oiseaux ou celles des chauves-souris (Shubin et al. 1997; Young and Hallgrímsson 2005; Hall 2010).

Limitations de l'étude

En ce qui concerne l'analyse de la covariation dans la présence/absence des nageoires, une limitation qui doit être prise en compte concerne les incertitudes quant aux relations d'homologie des nageoires entre les différents groupes de poissons. Ceci est particulièrement important pour les nageoires paires au niveau des agnathes où des hypothèses variées existent quant à l'homologie avec les nageoires pectorales et pelviennes des gnathostomes. À titre d'exemple, les résultats de l'analyse de

correspondance multiple pour les agnathes suggèrent que la covariation est faible quant à la présence/absence des différentes nageoires au sein de ce groupe. Ceci a été interprété comme résultant d'une période d'exploration des configurations possibles de nageoires parmi ces vertébrés basaux. Dans le codage des caractères utilisés, basé principalement sur des critères topographiques, seuls les pituriaspides, les ostéostracés et certains thélodontes ont été considérés comme possédant des nageoires pectorales, et aucun agnathe n'a été codé comme possédant des nageoires pelviennes. Certains auteurs ont cependant suggéré qu'une partie des nageoires paires chez les agnathes pourraient en fait constituer des précurseurs des nageoires pelviennes, notamment au sein des anaspides et des Furcacaudiformes (Moy-Thomas and Miles 1971; Janvier and Arsenault 2007; Wilson et al. 2007). Il importe donc de garder en tête que les résultats obtenus pour les agnathes auraient pu différer en considérant l'hypothèse que les nageoires allongées des anaspides et des thélodontes constituent des précurseurs des nageoires pelviennes.

Dans la même optique mais cette fois en ce qui concerne les acanthoptérygiens, les espèces possédant des nageoires dorsales séparées (p. ex. première dorsale épineuse séparée de la seconde dorsale rayonnée) ont été codées comme possédant deux nageoires dorsales. Ce codage semble en effet tout à fait intuitif et correspond bien avec l'hypothèse de Mabee et al. (2002) suggérant que la première nageoire dorsale épineuse des acanthoptérygiens résulte de la duplication du module de la nageoire dorsale postérieure rayonnée. Cependant, une hypothèse alternative est que la présence de deux nageoires dorsales, en apparence séparées l'une de l'autre, résulte de la régionalisation d'une nageoire dorsale ancestrale qui était continue (Sandon 1956; Janvier 1996b). Quoiqu'il en soit, cette interprétation ne change que peu de choses aux patrons de covariation observés. En effet, et à titre d'exemple, qu'il y ait correspondance entre les nageoires dorsales et anales parce qu'elles ont toutes deux été dupliquées, ou parce qu'elles sont toutes deux régionalisées, il n'en demeure pas moins qu'il y a une coordination dans leurs états de caractères.

Quelques limitations de l'étude sont également liées aux analyses de morphométrie géométrique. L'une de celles-ci concerne les landmarks utilisés au niveau des nageoires paires. En effet, il était possible de positionner moins de landmarks au niveau des points d'insertion des nageoires paires comparativement aux nageoires médianes. Ceci est particulièrement vrai pour les nageoires pelviennes qui, en raison de leur insertion ventrale sur le corps du poisson, n'étaient représentées que par un seul landmark. Il n'en demeure pas moins qu'à l'échelle microévolutive, plusieurs des hypothèses de modularité les mieux supportées suggèrent que les nageoires paires forment un module variationnel. Or, il est plus probable de concevoir qu'une limitation dans le nombre de landmarks aurait augmenté les chances de rejeter l'hypothèse de modularité plutôt que l'inverse. Des analyses incluant plus de landmarks au niveau des nageoires pectorales et pelviennes auraient donc été avantageuses et auraient pu contribuer à augmenter le support statistique pour un module variationnel des nageoires paires, en plus d'augmenter les chances d'identifier un module évolutif des nageoires paires.

Une autre limitation concernant les analyses de morphométrie géométrique résulte du fait que les landmarks et semi-landmarks ont dû être positionnés le long de la base des nageoires. Ce faisant, ils représentent des configurations quasi-linéaires et ne capturent que peu d'information sur la forme des nageoires. Cependant, au niveau des analyses, la superposition de Procrustes a été effectuée sur l'ensemble de la configuration de landmarks plutôt qu'individuellement pour chacune des partitions. Ainsi, les informations sur la taille et la position relative des partitions sont préservées et prises en compte dans les analyses. Il est raisonnable de considérer que, tout comme la limitation précédente, cette lacune dans l'échantillonnage de landmarks aurait contribué à réduire le support statistique pour les hypothèses de modularité plutôt que l'inverse. Plusieurs raisons expliquent le choix de cette stratégie d'échantillonnage, utilisant des landmarks à la base de l'insertion des nageoires. D'abord, les nageoires

des actinoptérygiens sont des structures avec de nombreux points d'articulation, si bien qu'il est impossible de standardiser leur extension et leur positionnement d'un spécimen à l'autre. Ainsi, la digitalisation de landmarks sur le pourtour externe de la nageoire aurait incorporé les différences dans la standardisation de la position de la nageoire par l'expérimentateur comme source importante de variation. Les spécimens conservés accumulent aussi fréquemment des dommages liés à la manipulation de ceux-ci, et qui se manifestent notamment au niveau des nageoires. Pour cette raison, la digitalisation de landmarks sur le pourtour extérieur des nageoires aurait aussi incorporé une seconde source de variation dans les analyses, cette fois liée à un artefact de préservation. Finalement, tel que mentionné, la stratégie d'échantillonnage et d'analyse des données incorpore l'information sur la position et la taille relative des partitions. Or, aussi bien pour les nageoires paires que médianes, une partie importante de la disparité morphologique au niveau de l'organisation des nageoires concerne justement des changements dans la position et dans la longueur de la base des nageoires sur le corps du poisson.

Perspectives de recherche dans le domaine concerné

Les résultats du premier chapitre de cette thèse doctorale ont permis de montrer que même avec des données semi-quantitatives (présence/absence et nombre de nageoires), il est possible d'identifier des patrons de covariation entre certaines paires de nageoires suggérant que celles-ci forment des modules évolutifs. Dans cette optique, il pourrait être intéressant de vérifier si des patrons de covariation existent aussi au niveau du nombre de structures de support exo- et/ou endosquelettiques. Une telle analyse pourrait être envisagée tant à l'échelle microévolutive qu'à l'échelle macroévolutive. De plus, Mabee et al. (2002) ont proposé qu'un module régissait le développement intégré entre les éléments exo- et endosquelettiques des nageoires médianes. L'utilisation de radiographies permettrait d'obtenir de l'information sur ces éléments de support endosquelettique, qui ne sont pas visibles en morphologie externe.

Les résultats du deuxième et du troisième chapitre suggèrent que malgré l'utilisation des mêmes stratégies d'échantillonnage par landmark et des mêmes méthodes pour tester des hypothèses de modularité, la correspondance n'est pas parfaite entre les modules variationnels observés chez deux Cyprinidae et les modules évolutifs identifiés à l'échelle des actinoptérygiens. Parmi les interprétations possibles, il a été suggéré que les modules évolutifs à si large échelle phylogénétique représentent un amalgame des patrons d'intégration morphologique de plusieurs lignées évolutives d'actinoptérygiens. À titre de perspective à court terme, il serait donc intéressant de réduire l'amplitude du spectre phylogénétique de l'aspect macroévolutif de l'analyse, et de vérifier si à l'échelle de la famille ou de l'ordre, les patrons d'intégration morphologique et de modularité sont conservés. À ces fins, les Cyprinidae et/ou les Cypriniformes seraient parmi les groupes ciblés, notamment pour permettre la comparaison avec les résultats obtenus pour le poisson-zèbre et le ventre rouge du Nord. La famille des Cichlidae serait un autre groupe de choix pour ce type d'analyse. En effet, les cichlidés ont fait l'objet de nombreux travaux dans les dernières décennies et sont considérés comme des organismes modèles dans l'étude des processus sous-jacents aux radiations adaptatives (Liem 1973, 1980; Albertson and Kocher 2001; Kocher 2004; Albertson and Kocher 2006). La littérature récente est donc abondante à leur sujet et de nombreuses phylogénies basées sur des échantillons considérables d'espèces sont disponibles (p. ex. Farias et al. 1999, 2001; Salzburger et al. 2002; Takahashi 2003; Day et al. 2008; López-Fernández et al. 2010; Friedman et al. 2013b).

De plus, dans le cadre du volet macroévolutif des analyses de modularité, toutes les espèces analysées avaient le même patron de configuration des nageoires, soit des nageoires dorsale et anale uniques, des nageoires pectorales et pelviennes, et une nageoire caudale. Ceci était nécessaire puisque l'un des prérequis des analyses en morphométrie géométrique est que l'ensemble des spécimens partagent le même nombre de landmarks homologues. Il serait donc particulièrement intéressant d'étudier

les patrons d'intégration morphologique et de modularité évolutive chez des espèces qui possèdent une seconde nageoire dorsale. Deux hypothèses semblent particulièrement envisageables. La première serait que la nageoire dorsale épineuse forme un module dont le positionnement est relativement indépendant des autres nageoires médianes, tel que suggéré par Mabee et al. (2002). Un tel résultat serait attendu si la nageoire dorsale épineuse représente un module dupliqué qui s'est subséquemment découplé au cours de l'évolution des acanthoptérygiens. La seconde hypothèse s'inspire des résultats obtenus dans le troisième chapitre de cette thèse doctorale. La nageoire dorsale épineuse pourrait alors participer au module évolutif du tronc avec les autres nageoires paires et médianes, à l'exclusion de la nageoire caudale. L'utilisation de radiographies plutôt que de photographies pourrait être un outil souhaitable lors de la digitalisation des landmarks puisqu'elle permettrait d'inclure dans l'échantillon des espèces chez lesquelles la nageoire dorsale épineuse demeure rattachée par une membrane à la nageoire dorsale postérieure, supportée par des rayons. Les radiographies permettraient ainsi de déterminer adéquatement la zone de transition où s'opère le changement de type de support exosquelettique.

Recherches futures

Parmi les directions futures envisagées, une avenue intéressante repose dans l'utilisation d'imagerie par tomodensitométrie plutôt que des photographies des spécimens. Cette méthode permet de reconstruire un modèle virtuel de l'anatomie interne et externe d'un spécimen en utilisant les différences de densités entre les structures (Cormack 1963; Hounsfield 1973; Abel et al. 2012). L'un des avantages de cette méthode est qu'elle permet l'obtention d'une image tridimensionnelle (3D) à haute résolution de l'anatomie complète des spécimens (Abel et al. 2012), ce qui apporterait une précision supplémentaire aux données de morphométrie géométrique comparativement à des photographies nécessairement bidimensionnelles (2D). La majorité des méthodes utiles pour analyser des patrons d'intégration morphologique et

tester des hypothèses de modularité fonctionnent par ailleurs tout aussi bien en 2D et en 3D. Un avantage supplémentaire dans l'utilisation de la tomodensitométrie découle du fait que les points de jonctions des structures osseuses ou cartilagineuses deviennent visibles, ce qui augmente considérablement le nombre de landmarks qui peuvent être positionnés. Ainsi il deviendrait possible d'analyser des patrons d'intégration et de modularité dans d'autres régions fonctionnellement importantes du corps, notamment au niveau de la tête. Le Laboratoire de Paléontologie et de Biologie évolutive dirigé par le Dr. Cloutier a d'ailleurs accès à un tel appareil de micro CT scan permettant de faire des lectures par tomodensitométrie.

De plus une poursuite de la collaboration étroite entre moi-même, Dr. Richard Cloutier et Dr. Miriam L. Zelditch est prévue dans le cadre d'un projet à long terme dont l'un des objectifs est d'analyser les patrons de disparification morphologique et écologique au cours de la radiation évolutive des gnathostomes basaux. Dans ce contexte, les expertises que j'ai eu l'opportunité de développer pendant la complétion de ma thèse, notamment en ce qui concerne les outils de la morphométrie géométrique, seront un atout majeur afin de poursuivre cet objectif.

ANNEXE A

HOW TO DEFINE A FIN?

Before we can investigate patterns of morphological disparity regarding the presence or absence of the different fins, it is crucial to provide a definition for each fin. Surprisingly, a clear definition of what constitutes a "fin" is uncommon in recent literature. For this purpose, we provide a brief overview on how fins have been described historically after which we will statute on our understanding of this term for the purpose of this paper.

For centuries, it has been recognized that a common character of fishes is that they generally have fins. Although Aristotle did not provide a clear definition of the term "fin", he observed that fins were essentially organs of locomotion and that fishes displayed much disparity in their fin configurations (Aristotle et al. 1878; Aristotle and Barthélémy-Saint-Hilaire 1883). In 1770, Goüan defined fins as parts composed of a series of rays or spines, covered and united by a membrane, that project from the body and are used to accomplish all of the different movements necessary for swimming. He further distinguished true fins from appendages that he designated as "false fins," the latter being simple folds of skin without spines or rays. De Lacépède used a similar definition while adding that some fishes possess membranes without rays or rays without membranes and that these should nonetheless be termed fins owing to their position and/or function (Lacépède 1798; Lacépède et al. 1853).

Fins can be separated into two categories: median (or unpaired) and paired fins. From a morphological and structural standpoint, Owen (1854) and Huxley (1871) considered that median fins consist of skin folds that are supported by dermal bones termed rays or spines. However, both authors referred to the low median folds of integument present in the dorsal and caudal regions of cephalochordates and lampreys as

homologous to the median fin system of other fishes. Goodrich (1909, p. 71) described the median fins as "*longitudinal median structures, internally segmented like the body itself, and involving many segments*." Goodrich (1909) considered that fin metamerism is evident from the internal skeleton that is composed of a series of rays equal in number or a multiple of the number of neural arches or their musculature. Many authors (Lacépède 1798; Cuvier and Valenciennes 1828; Cuvier 1849; Lacépède et al. 1853) instead provided functional definitions of the median fins comparing them to the keels or rudders of boats.

A number of fins are part of the median-fin system and these have been distinguished mostly in terms of their position on the body. Dorsal fins are located on the dorsal midline between the head and the tail, anal fins are located along the ventral midline between the anus (or cloaca) and the tail, and the caudal fin is located at the extremity of the tail (Goüan 1770; Lacépède 1798; Lacépède et al. 1853; Huxley 1871; Günther 1880). Some taxa bear additional fins along the midline. Dorsally, a number of actinopterygians have an adipose fin. Günther (1880) used the term "fatty fin" and defined it as a dorsal rayless fold of skin in which fat is deposited. More recently the adipose fin has been described as a small non-rayed fin usually located medially between the dorsal and caudal fins, and variably present among several groups of basal euteleosts (Reimchen and Temple 2004). Although the finrays are generally absent, the adipose finweb is nonetheless supported by proximo-distally oriented rods of collagen, termed actinotrichia (Stewart and Hale 2013; Stewart et al. 2014). Two additional forms of dermal skeleton can be found in the adipose fin of some Siluriformes and Characiformes: anterior spines derived from modified scutes, and true fin rays (Stewart et al. 2014; Stewart 2015). In some of these euteleost taxa, a ventral adipose fin is also described (Greenwood et al. 1966; Fischer and Bianchi 1984). Furthermore, in many agnathan fishes, a median ventral finfold can be found, positioned anteriorly to the cloaca and of variable extent.

In gnathostomes, the paired fins comprise the pectoral and pelvic fins. Belon (1551) and Rondelet (1558) characterized the pectoral and pelvic fins as "wings" that fishes use "to fly" through the water. As with the median fins, some authors have used topological criteria to distinguish both sets of paired fins: the pectoral fins are located closely behind the gill openings, whereas the pelvic or ventral fins, even though they display more disparity in their position, are inserted on the abdomen and always anteriorly to the anus (Goüan 1770; Cuvier and Valenciennes 1828; Cuvier and Duméril 1835; Cuvier 1849; Günther 1880). Paired fins have also been defined in light of their homology with the fore- and hindlimbs of tetrapods (Cuvier and Valenciennes 1828; Cuvier and Duméril 1835; Owen 1846; Cuvier 1849; Owen 1849, 1854; Huxley 1871; Günther 1880). Owen (1849) considered that both the anterior and posterior members are structures supported by inverted arches: the pectoral fins are supported by the scapular arch (i.e. pectoral girdle) and the pelvic fins by the pelvic arch (i.e. pelvic girdle). Owen's definitions of pectoral and pelvic appendages are thus strongly based on the nature of the appendicular skeleton and its relative positioning, even though he acknowledged that the position is frequently variable (Owen 1854). Huxley (1871, p. 2) did not define the paired fins *per se* but stated that vertebrate paired limbs "*are always provided with an internal skeleton, to which the muscles moving the limbs are attached*." Howell (1933) instead proposed a functional context for the appearance of the paired fins, suggesting that the pectoral fins were owing to a requirement of voluntary movement for progression, whereas the pelvic fins evolved mainly for involuntary static action for support or balance. Some authors consider that true paired fins must be inserted on an endoskeletal girdle, they must be supported by a series of endoskeletal (basals and radials) and exoskeletal (fin rays) elements (Janvier 1996a; Wilson et al. 2007). Johanson (2010) added that, at least in gnathostomes, the movement of the paired fins are under muscular control and that they are generally narrow-based. Some taxa, mostly agnathans, possess additional lateral folds of skins that do not conform to the definitions of pectoral and pelvic fins provided above (these are variously referred to as ventrolateral folds, paired finflaps, suprabranchial fins, etc.)

For the purpose of this study, we will use a definition of fins analogous to that of De Lacépède, thus we will consider that finfolds without endoskeletal support should also be termed fins. As for the identity of the fins, we will emphasize positional criteria: dorsal fins are located on the dorsal side, anal fins are on the ventral side between the anus and the tail, and the caudal fin is at the extremity of the tail. Some species present additional unpaired finfolds that can be inserted either anteriorly (e.g., some Myxiniformes) or posteriorly to the cloaca (e.g., some Paralepididae): these will be termed “median ventral fins.” As for the paired appendages, we will consider that the pectoral fins are inserted on the thorax close to the gill openings, the pelvic fins are ventrally inserted in front of the cloaca, and that both need to be narrow-based. Other paired structures, either in the form of long ribbon-like folds or serially repeated fin supports, will be termed "ventrolateral paired fins."

ANNEXE B

A HISTORICAL ACCOUNT OF APPENDAGE DIVERSITY AND HOMOLOGY AMONG BASAL CHORDATES

(1) Basal chordates

Chordates comprise three subphyla: Cephalochordata, Tunicata and Craniata (including Vertebrata). Based on shared morphological characters, the cephalochordates have long been considered as the sister-group to craniates (e.g., Herdman 1904; Garstang 1928; Maisey 1986; Schaeffer 1987; Shimeld and Holland 2000; Rowe 2004). However, an alternate hypothesis has also been proposed whereby tunicates, and not cephalochordates, are the sister group to craniates (Jefferies 1973; Jefferies and Lewis 1978; Jefferies 1979, 1986), a view that is well supported by many recent molecular-based phylogenetic analyses (e.g., Blair and Hedges 2005; Philippe et al. 2005; Bourlat et al. 2006; Delsuc et al. 2006; Delsuc et al. 2008; Dunn et al. 2008; Putnam et al. 2008; Singh et al. 2009; Heimberg et al. 2010).

The extant representatives of the Cephalochordata are the Amphioxiformes, or lancelets, which include between 30 and 35 species divided into two genera (Hubbs 1922; Poss and Boschung 1996; Stokes and Holland 1998; Satoh et al. 2014). Lancelets possess a finfold along the dorsal and ventral midlines of the body that is continuous around the tip of the tail, as well as along the anterior tip of the notochord, where it forms a "rostral fin" (Rice 1880; Jordan and Gilbert 1882; Lankester 1889; Andrews 1893; Wiley 1894; Kirkaldy 1895; Jordan and Evermann 1896; Jordan and Snyder 1901; Herdman 1904; Goodrich 1930; Bigelow and Farfante 1948; Jefferies 1986; Holland and Holland 1991). Schaeffer (1987) suggested the median finfold of lancelets to be homologous with the larval median finfold of developing vertebrates. Some authors describe the median ventral finfold as an anal fin (e.g., Goodsir 1844; Jordan

and Evermann 1896; Jordan and Snyder 1901) while others use the term preanal fin (e.g., Hubbs 1922; Xu et al. 2005). We concur with the latter opinion since the ventral finfold is inserted anteriorly to the anus. Rod-like structures along the dorsal and ventral fins have sometimes been interpreted as finrays (e.g., Yarrell 1836; Lankester 1889; Andrews 1893; Wiley 1894; Goodrich 1930; Bigelow and Farfante 1948; Jefferies 1986). It is now clear that these so-called finrays of lancelets are not homologous to the radials or dermal rays of vertebrates (Holland and Holland 1991; Holland and Chen 2001). They are in fact retroperitoneal accumulations of haemal fluid containing nutritional reserves that project into coeloms along the median finfolds; they shrink and disappear during gametogenesis or if the individuals are subjected to starvation (Azariah 1965; Holland and Holland 1991; Stokes 1996). Paired structures, termed metapleural folds, arise posteriorly to the oral hood, extending ventrolaterally under the branchial region and atrial cavity (Goodsir 1844; Lankester 1875; Rice 1880; Lankester 1889; Andrews 1893; Wiley 1894; Kirkaldy 1895; Herdman 1904; Goodrich 1930; Jefferies 1986). Posteriorly, the left metapleural fold is continuous with the median ventral fin in *Epigonichthys*, whereas both metapleural folds are interrupted behind the atriopore in *Branchiostoma* (Kirkaldy 1895; Poss and Boschung 1996). Thacher (1877) suggested that the metapleural folds were homologous to the continuous lateral finfolds from which pectoral and pelvic fins are hypothesized to have evolved. However, these metapleural folds are not functionally used as fins in extant cephalochordates (Wiley 1894). Furthermore, they are hollow structures that are filled with fluid (Lankester 1875; Rice 1880; Lankester 1889; Wiley 1894), and they become flattened and inconspicuous during the spawning season when the atrial cavity is distended owing to the increasing space occupied by the developing gonads (Lankester 1875; Rice 1880; Lankester 1889).

Tunicates, or urochordates, comprise three classes and about 3000 species (Shenkar and Swalla 2011; Satoh et al. 2014). As adults they are sac-like marine filter-feeding organisms, yet a post-anal tail and finfold is present during the larval stage in two of

the classes, the Ascidiacea and Thaliacea, and persists during the entire life cycle in representatives of the third class, the Appendicularia (Herdman 1904; Cloney 1982; Nishino and Satoh 2001). The tail includes the notochordal axis, muscle fibers, as well as dorsal and ventral finfolds that are continuous around the posterior tip of the notochord (Kowalevsky 1866; Herdman 1904; Berrill 1930; Cloney 1982; McHenry 2005). Tunicates are hypothesized to have arisen during or even before the Cambrian diversification, however their fossil record is very poor owing to the absence of mineralized parts: the only undisputed tunicate species is from the Lower Cambrian (Chen et al. 2003).

The fossil record also contains a few forms which have variously been interpreted as stem deuterostomes, cephalochordates, stem chordates, or stem craniates (*Yunnanozoon lividum*, *Haikouella lanceolata*, *H. jianshanensis*, *Pikaia graciliens*, *Cathaymyrus diadexus*). *Yunnanozoon,* from the Lower Cambrian of southern China, was originally interpreted as a worm-like animal bearing a segmented cuticle (Hou et al. 1991). Although some authors have suggested a cephalochordate affinity (e.g., Chen et al. 1995; Stokes and Holland 1998), it seems more likely that *Yunnanozoon* is a lower deuterostome unrelated to craniates or vertebrates (e.g., Bergström et al. 1998; Shu 2003; Shu 2008; Shu et al. 2010). Dorsal and ventral dark bands along the midline of the animal (Chen et al. 1995; Dzik 1995) have been interpreted as dorsal and ventral finfolds (Chen et al. 1995). Shu, Zhang & Chen (1996b) interpreted the existence of a much larger sclerotized and segmented dorsal fin, a view which has been disputed based on recent evidence from the closely allied *Haïkouella* suggesting that the segments are actually myomeres (Mallatt and Chen 2003; Mallatt et al. 2003). Paired ventrolateral folds are observable on many specimens (Dzik 1995; Chen and Li 1997) and have been compared to the metapleural folds of cephalochordates (Chen and Li 1997). Based on the morphology of *Haïkouella, Y. lividum* has occasionally been reconstructed as having a caudal process bearing a finweb (e.g., Chen and Huang 2006;

Chen and Huang 2008). However, Chen and Huang (2008) acknowledge that this structure has not been observed in any of the specimens of *Yunnanozoon*.

Haikouella is known from hundreds of complete specimens from the Lower Cambrian of southern China (Chen et al. 1999). Some specimens of *Haikouella* present a post-anal tail (referred to as a "caudal process") posteriorly to the anus, a structure which is hypothesized to break off during fossilization (Chen et al. 1999; Mallatt and Chen 2003). An alternate view is that the caudal process is a taphonomic artefact brought about by folding and compaction of the posterior part of the body (Shu and Morris 2003). Medially, there are also dorsal and ventral fins but lateral appendages are entirely absent (Holland and Chen 2001). The fins in *Haikouella* do not contain rays (Mallatt and Chen 2003). Similarly to *Yunnanozoon*, the phylogenetic position of *Haikouella* is debated. On the one hand, this taxon might be a stem deuterostome (Shu 2003; Shu and Morris 2003; Shu et al. 2003b; Shu 2008; Shu et al. 2010). Alternatively, it might be a stem craniate if the interpretation of structures identified as a brain, eyes, a post-anal tail and median fins are correct (Chen et al. 1999; Mallatt and Chen 2003; Mallatt et al. 2003). It is nonetheless generally agreed that *Yunnanozoon* and *Haikouella* are close relatives (Mallatt and Chen 2003; Mallatt et al. 2003; Shu and Morris 2003; Shu et al. 2003b). Alternatively, they might also be synonyms (Turner et al. 2010). Results of phylogenetic analyses suggest that yunnanozoans are the sister group of craniates (Holland and Chen 2001; Mallatt and Chen 2003).

Pikaia, from the Middle Cambrian Burgess Shale of western Canada, was originally interpreted as a polychaete owing to the presence of curious lateral appendages in the branchial area (Walcott 1911, 1931). Subsequent investigations of the material revealed chordate-like characters (Morris 1979; Morris and Whittington 1979; Insom et al. 1995), and *Pikaia* has since been interpreted as closely related to cephalochordates (e.g., Stokes and Holland 1998; Shu et al. 1999; Smith et al. 2001) or to yunnanozoans (Morris and Caron 2012). A thorough re-examination of the *Pikaia*

material was recently published where the only appendages described are a dorsal finfold which is not supported by rays and a series of nine bilaterally arranged appendages with possible pharyngeal pores near their insertions (Morris and Caron 2012). There is also a ventral keel extending from just behind the last of the lateral appendages and becoming less distinct posteriorly which might have represented a ventral fin, or possibly a gonadal structure (Morris and Caron 2012). Mallatt and Holland (2013, p. 268) argued that the ventral keel and posterior ventral area are most definitively a fin because they "*look fin-like and seem to be homologues of a fin.*" Although a tail fin devoid of finrays has been mentioned in some descriptions (Briggs and Kear 1994; Insom et al. 1995; Smith et al. 2001), this feature is absent in Morris & Caron (2012)'s detailed revision of the material.

Cathaymyrus was originally described based on a single specimen from the Lower Cambrian of southern China (Shu et al. 1996a). *Cathaymyrus* has been interpreted as lacking any evidence for fins or finrays (Shu et al. 1996a; Smith et al. 2001), although a dorsal fin is explicitly mentioned in Shu (2003). It has been suggested that *Cathaymyrus* might actually be a crushed specimen of *Yunnanozoon*, however this hypothesis was later discredited (Luo et al. 2001; Shu et al. 2001; Shu et al. 2010). *Cathaymyrus* is generally interpreted as belonging to cephalochordates (Stokes and Holland 1998; Morris 2006; Shu 2008; Mallatt and Holland 2013).

(2) Stem vertebrates

Four Cambrian representatives of stem vertebrates (*Zhongjiangichthys rostratus*, *Myllokunmingia fengjiaoa*, *Haikouichthys ercaicunensis, Metaspriggina walcotti*) are sufficiently well known in terms of their fin configurations. Common to all four species is the absence of paired fins. Preanal and dorsal fins are present in *Zhongjiangichthys* (Shu 2003), *Myllokunmingia* (Shu et al. 1999; Holland and Chen 2001; Hou et al. 2002; Shu 2008) and *Haikouichthys* (Shu et al. 1999; Holland and Chen 2001; Hou et al.

2002; Shu et al. 2003a; Zhang and Hou 2004; Shu 2008). In the original descriptions of *Myllokunmingia* and *Haikouichthys*, doubts were expressed concerning the interpretation of a ventral feature which could have been either a median ventral finfold or paired ventrolateral finfolds (Shu et al. 1999; Shu et al. 2001). Subsequent discoveries and analyses of additional specimens of *Haikouichthys* provided no indications whatsoever that the ventral finfold is a paired structure (Hou et al. 2002; Shu et al. 2003a; Zhang and Hou 2004; Shu 2008). A dorsal fin was originally considered to be absent in *Metaspriggina* (Simonetta and Insom 1993). Later, a narrow area along the anterior trunk of the lectotype was interpreted as a possible dorsal fold or ridge (Morris 2008). The most recent revision of the *Metaspriggina* material suggests that it was entirely finless with the exception of a keel-like structure along the ventral midline; the authors mentioned however that the absence of fins could be a taphonomic artefact (Morris and Caron 2014). With the exception of *Zhongjiangichthys* where this character cannot be determined, a true anal fin is absent in all of these taxa. A caudal fin is present in *Haikouichthys* and absent in *Metaspriggina*; its presence cannot be assessed for the two other species.

Myllokunmingia, *Haikouichthys* and *Zhongjiangichthys* are considered as close relatives and have been assigned to the order Myllokunmingiida (Shu 2003). They are either interpreted as stem craniates (Shu 2003; Shu et al. 2003a) or as stem vertebrates (Shu et al. 2001; Shu 2005). It has been suggested that *Myllokunmingia* and *Haikouichthys* might be synonyms (e.g., Hou et al. 2002; Janvier 2007; Turner et al. 2010; Blieck 2011; Žigaitė and Blieck 2013), while other authors consider that these taxa are correctly identified as separate species (Shimeld and Holland 2000; Morris 2006; Morris and Caron 2012). *Zhongianichthys* has also been proposed as a possible synonym and badly preserved specimen of *Myllokunmingia* (Janvier 2007; Blieck 2011; Žigaitė and Blieck 2013) or *Haikouichthys* (Morris and Caron 2012). Recently, Morris & Caron (2014) argued for placing *Metaspriggina* among vertebrates based on

the presence of a notochord, camerular eyes, paired nasal sacs, a possible cranium, possible arcualia, W-shaped myomeres and a post-anal tail.

(3) Myxiniformes

Myxines, or hagfishes, are the most primitive craniates and comprise a single order, with about 79 living species (Zintzen et al. 2015) and three extinct species from the Late Carboniferous, two of which are only tentatively assigned to the Myxiniformes (Bardack and Richardson 1977; Bardack 1991, 1998; Poplin et al. 2001; Germain et al. 2014). Myxines have a simple fin configuration that most often includes a caudal fin supported by cartilaginous finrays (Adam and Strahan 1963; Wright et al. 1998) and a ventral preanal finfold (Fernholm 1998). However, the caudal fin can be absent in some extant hagfishes. For instance in *Myxine formosana*, the caudal fin is described as vestigial to absent (Mok and Kuo 2001; McMillan and Wisner 2004). Myxines generally lack a dorsal fin, although in the Carboniferous *Myxinikela siroka*, a dorsal fin arises somewhat anterior to the mid-body and is continuous with the caudal fin posteriorly (Bardack 1991, 1998). However, Bardack (1991, 1998) mentioned that the specimen might represent a juvenile stage of development.

The preanal finfold of myxines is devoid of internal skeletal support (Hardisty 1979) and is in fact a band of thin fleshy tissue found along the ventral midline starting from the cloaca and differing among species in its anterior extent (Wisner and McMillan 1995). The presence and conspicuity of the preanal finfold can also vary intraspecifically: in some species, it is reported either as weakly-developed, vestigial, or absent (e.g., Wisner and McMillan 1988, 1990; Kuo et al. 1994; McMillan and Wisner 2004). The preanal finfold is reported absent in the extant *Myxine debueni* (Wisner and McMillan 1995; Fernholm 1998) as well as in the Carboniferous *Gilpichthys greenei*, a fossil species which lacks all types of fins including the caudal fin (Bardack and Richardson 1977). It should be mentioned that *Gilpichthys* is known

from a single specimen and its assignment to the Myxiniformes has been debated: it might in fact constitute an immature organism (Bardack and Richardson 1977; Bardack 1998). However, a recent phylogenetic analysis reaffirmed its assignment as a stem hagfish (McCoy et al. 2016).

Paired fins are most often considered as entirely absent in Myxiniformes although both species of *Neomyxine* present lateral folds of skin located immediately above the gill openings (Richardson 1953, 1958; Zintzen et al. 2015). Contrary to the paired fins found in most other craniates, these "ventrolateral branchial finfolds" are thus located dorsally to the branchial openings and do not seem to be used in swimming but rather as support when individuals settle on substrate (Richardson 1953; Adam and Strahan 1963; Janvier 1978). Furthermore, there are no traces of internal skeletal support or of an associated specialized musculature (Forey 1984). Because *Neomyxine* is not resolved as the most basal of hagfish genera (Zintzen et al. 2015), this structure is unlikely to be homologous to the paired fins of other vertebrates (Donoghue et al. 2000).

(4) Petromyzontiformes

Petromyzontiformes, or lampreys, also comprise a single order including 43 living species and five fossil species (Renaud 2011; Chang et al. 2014; Hume et al. 2014). The oldest fossil lamprey is *Priscomyzon riniensis* from the Upper Devonian of South Africa (Gess et al. 2006). The caudal fin is always present in extant lampreys, with the exception of a single specimen of *Lampetra planeri* that was described as having an incompletely formed caudal fin (Hume et al. 2014). Among fossil lampreys, the caudal fin is absent only in *Pipiscius zangerli* (Bardack and Richardson 1977). Although the affinity of *Pipiscius* to the petromyzontids has been questioned (Janvier and Lund 1983; Bardack 1998), a recent phylogenetic analysis places this taxon among stem

lampreys (McCoy et al. 2016). However, a yolk sac might be present, suggesting that *Pipiscius* could in fact represent a larval organism (Bardack and Richardson 1977).

Most extant species have two dorsal fins, with the exception of all species belonging to *Ichthyomyzon* who have a single dorsal fin (Renaud 2011). As for fossil lampreys, most species have a single dorsal fin (Bardack and Zangerl 1968; Chang et al. 2006; Gess et al. 2006; Chang et al. 2014; McCoy et al. 2016), although *Hardistiella montanensis* has two dorsal fins (Janvier and Lund 1983; Janvier et al. 2004b). Anal fins have been described only in two fossil species, *Hardistiella* (Janvier and Lund 1983) and *Mayomyzon pieckoensis* (Bardack and Zangerl 1968). In *Hardistiella*, a small notch separates the chordal lobe of the caudal fin from the anal fin (Janvier and Lund 1983). Later, Janvier & Arsenault (2007) expressed that the presence of an anal fin required confirmation in this species. As for *Mayomyzon*, the dorsal, caudal and anal fins are continuous along the body, the latter being separated from the caudal fin by a small notch (Bardack and Zangerl 1968). Janvier & Lund (1983) questioned the presence of a true anal fin in *Mayomyzon* and suggested that this might instead be the typical anal crest found in present-day lampreys. In extant species, the anal fin is always absent although some specimens of *Petromyzon marinus* have been known to develop an anal fin, interpreted as an atavism (Vladykov 1973; Vladykov and Kott 1980; Janvier 1996a, 2007, 2008). Hume et al. (2014) also reported the presence of an anal fin supported by five or six finrays in a single specimen of the living *Lampetra planeri*. Spawning female lampreys develop fleshy pre- and post-anal fin-like folds prior to reproduction (Pletcher 1963; Hardisty and Potter 1971; Vladykov 1973; Vladykov and Kott 1980; Janvier and Lund 1983; Kott et al. 1988; Renaud 2011). This temporary structure, present only in females during spawning, is not considered as an anal or preanal fin. Similarly, the base of the two dorsal fins becomes swollen in a way that makes them appear united (Hardisty and Potter 1971; Kott et al. 1988; Renaud 2011). Again, because this is a temporary condition, these taxa are nonetheless considered as

having two distinct dorsal fins. A preanal finfold, such as was described for myxines, is always absent in lampreys.

Paired fins are entirely lacking in all fossil and extant lampreys. Janvier (1981b) suggested that the absence of paired fins is most likely secondary in Petromyzontiformes because closely related groups (e.g., anaspids and osteostracans) have them. In support of this palaeontological hypothesis, it was recently shown that the absence of paired fins in lampreys could be traced back to ventrally migrating extensions of the dermomyotome, effectively separating the lateral plate mesoderm from the overlying ectoderm (Tulenko et al. 2013). In tetrapods, the proper development of many elements of the paired limbs and girdles are known to require signaling between the ectoderm and the lateral plate mesoderm (Capdevila and Izpesúa Belmonte 2001; Ehehalt et al. 2004; Malashichev et al. 2005; Wang et al. 2005; Malashichev et al. 2008). Tulenko et al. (2013) further suggest that the persistence of somatic lateral plate mesoderm external to the myotomes was a key step towards the development of paired fins in gnathostomes.

A final representative of the Petromyzontiformes requires separate mention owing to its uncharacteristic morphology, *Tullimonstrum gregarium*. *Tullimonstrum,* from the Late Carboniferous of Illinois, USA., was originally described as a worm-like animal (Richardson 1966), and its relationship to annelids, molluscs or arthropods have been considered [see Turner et al. (2010) for a review of these hypothesized relationships]. Based on a re-examination of over 1200 specimens and the inclusion of the reinterpreted characters into a phylogenetic analysis, *Tullimonstrum* is now considered as a stem lamprey (McCoy et al. 2016). *Tullimonstrum* possesses a single long and low dorsal fin, as well as an asymmetrical oblanceolate caudal fin (Clements et al. 2016; McCoy et al. 2016).

(5) Conodonta

The conodont fossil record extends from the Upper Cambrian to the Upper Triassic (Aldridge and Smith 1993). Depending on classification, conodonts comprise between five and seven orders, most of which are known only from remains of the oral apparatus (Sweet 1988; Dzik 1991; Aldridge and Smith 1993; Aldridge et al. 1995). Although there are close to 5000 named species, Sweet (1988) estimated that 1446 species in 246 genera represent a more conservative figure. Only a few species are known from articulated specimens, exceptionally showing preservation of some of the soft tissues anatomy: one of these is *Promissum pulchrum*, known only from well-preserved material from the anterior portion of the animal (Aldridge and Theron 1993; Gabbott et al. 1995), and two others belong to the genus *Clydagnathus* [*C. windsorensis* and *Clydagnathus*? sp. (*C.*? sp. cf. *C. cavusformis*)] (Briggs et al. 1983; Aldridge et al. 1986; Aldridge et al. 1993). In the latter species, the elements of the conodont apparatus most useful for identification purposes remain for the most part buried in the sediment: Briggs et al. (1983) tentatively assigned the material to *C. cavusformis* on the basis of general similarities, while expressing their uncertainty in that respect.

Because there are so few well-preserved specimens with postcranial material preserved, little is known concerning the fin configurations in conodonts. The tail region is preserved in some of the *Clydagnathus* material and shows a well-developed caudal fin supported by finrays (Briggs et al. 1983; Aldridge et al. 1986; Briggs 1992; Aldridge et al. 1993; Aldridge and Purnell 1996; Pridmore et al. 1997). In *C. cavusformis*, there is a gap in the finrays along the dorsal midline, followed anteriorly by a second series which is interpreted as a dorsal fin (Briggs et al. 1983; Aldridge et al. 1986). Indications as to the presence of other median or paired fins have not been found.

The affinity of conodonts is still strongly debated. Until the discovery of some specimens with elements of the soft anatomy preserved (Briggs et al. 1983; Aldridge et al. 1986; Aldridge 1987; Gabbott et al. 1995), they had been interpreted as belonging to a number of invertebrate and vertebrate groups [see Aldridge et al. (1993) for a review of previously hypothesized conodont interrelationships], or assigned to a separate phylum (Sweet 1988). Current views are that they are either basal chordates (Aldridge et al. 1986; Aldridge 1987; Aldridge and Briggs 1990; Pridmore et al. 1997; Blieck et al. 2010; Turner et al. 2010), or basal vertebrates (Briggs 1992; Aldridge and Theron 1993; Briggs and Kear 1994; Gabbott et al. 1995; Purnell 1995; Aldridge and Purnell 1996; Donoghue et al. 1998; Donoghue et al. 2000; Sweet and Donoghue 2001; Schubert et al. 2006).

(6) Pteraspidomorphi

The extinct Pteraspidomorphi comprise four orders (Astraspidiformes, Arandaspidiformes, Cyathaspidiformes and Pteraspidiformes), most of which are known only from the remains of the cephalothoracic shield. The Astraspidiformes currently include only two extinct species from the Ordovician of North America and Siberia (Janvier 1996a, b), among which *Astraspis desiderata* is the best known. *Astraspis* has a caudal fin but no other median or paired fins (Lehtola 1983; Elliott 1987; Soehn and Wilson 1990; Gagnier 1993a, b; Sansom et al. 1997). Some of the earliest undisputed vertebrate remains, from the Lower Ordovician of Australia, have been assigned to the arandaspid genus *Porophoraspis* (Young 1997). However, articulated postcranial material is known only for two species of Arandaspidiformes, *Sacabambaspis janvieri* from the Middle-Late Ordovician of Bolivia (Gagnier et al. 1986; Gagnier 1989; Gagnier and Blieck 1992; Gagnier 1993b; Pradel et al. 2007) and *Arandaspis prionotolepis* from the Early-Middle Ordovician of Australia (Ritchie and Gilbert-Tomlinson 1977; Ritchie 1985). In *Sacabambaspis*, a caudal fin is present and there are dorsal and preanal crests and ridge scales along the dorsal and ventral midlines

(Gagnier and Blieck 1992; Gagnier 1993a, b). As for *Arandaspis*, even in the best-preserved specimen, only a small part of the body posteriorly to the cephalothoracic shield is preserved so that nothing can be said concerning the shape and arrangement of the fins (Ritchie and Gilbert-Tomlinson 1977; Ritchie 1985).

The Cyathaspidiformes and Pteraspidiformes are generally referred to as heterostracans. Heterostracans appeared in the Lower Silurian and their stratigraphic range extends to the Upper Devonian (Janvier 1996b; Žigaitė and Blieck 2013). They are extremely conservative in terms of fin configurations: all median and paired fins are absent with the exception of the caudal fin (White 1935; Stensiö 1964). Lateral extensions of the shield are present in some taxa and would have served as an aid in stability (the cornual plates of pteraspids and branchial plates of psammosteids) but these structures were generally not movable (Westoll 1958; Halstead 1973; Halstead and Turner 1973; Janvier and Blieck 1979), with the possible exception of the branchial plates in *Psammosteus kiaeri* (Tarlo 1964, 1965). Some authors (Stensiö 1964; Janvier and Blieck 1979; Blieck 1984) have suggested that heterostracans retain a preanal finfold in the form of a ventral crest composed of scales. Stensiö (1964) also interpreted the median dorsal crest scales as representing a dorsal finfold. We consider these interpretations unlikely since scales or scutes arranged along the midline are present in other taxa and they are unquestionably not considered as fins [e.g., sturgeons (Acipenseriformes) and lumpsuckers (Cyclopteridae) have dorsal scutes; anchovies, herrings and sardines (Clupeiformes) generally have ventral scutes].

(7) Anaspida

The stratigraphic range of the Anaspida extends from the Lower Silurian to the Upper Devonian (Janvier 1996b; Blom et al. 2002). Anaspids comprise two or three orders depending on classifications, and about 25 genera. Some authors consider that true anaspids are only those taxa that possess tri-radiate post-branchial spines: this includes

the scaled anaspids, or birkeniids, and members of the genus *Lasanius* (Arsenault and Janvier 1991; Janvier 1996b, c; Blom et al. 2002; Blom 2012). We favoured the more inclusive view whereby the "naked-anaspids" or Jamoytiiformes, a group that shares with other anaspids the possession of a strongly hypocercal tail, are nested within the Anaspida (von Zittel and Woodward 1902; Kiaer 1924; Stensiö 1939; Robertson 1941; Blom and Märss 2010; Keating and Donoghue 2016).

Anaspids present some challenges as to the interpretation of their fin configurations. All sufficiently known anaspids possess at least a caudal fin and an anal fin. These fins were supported by radials that were most likely under muscular control (Jarvik 1959). The presence of a preanal fin has also been suggested for a few species (e.g., *Birkenia*, *Kerreralepis, Pterygolepis*) (Blom 2012). A long and low dorsal fin has been described for *Achanarella trewini* (Newman 2002), *Endeiolepis aneri* (Stensiö 1939; Robertson 1941; White 1946; Arsenault and Janvier 1991; Newman and Trewin 2001) and *Jamoytius kerwoodi* (White 1946; Ritchie 1968a; Janvier 1981b). In *Euphanerops longaevus*, a dorsal fin has been reported either as present (Woodward 1900a; Stensiö 1939; Arsenault and Janvier 1991) or absent (Janvier and Arsenault 2007; Sansom et al. 2013). A recent re-investigation of the *Euphanerops* material confirms that a long and low dorsal fin is indeed present (M. Chevrinais, pers. comm.; R.C. pers. observ.) Furthermore, it has been proposed that *E. aneri* might actually represent a junior synonym for *E. longaevus* (Janvier et al. 2006; Janvier and Arsenault 2007; Janvier 2008; Sansom et al. 2013). In other anaspids, the dorsal fin is generally absent although some consider that the series of dorsal and/or ventral scutes represent reductions of what was originally dorsal or ventral finfolds (Stensiö 1939; Ritchie 1964; Stensiö 1964; Ritchie 1968a; Moy-Thomas and Miles 1971; Forey 1995). Another opinion is that the large epichordal lobe of the caudal fin is in fact homologous to the second dorsal fin found in lampreys, osteostracans and gnathostomes (Jarvik 1959; Janvier 1981b; Arsenault and Janvier 1991; Janvier 1996b, 2007, 2008; Blom and Märss 2010).

Many anaspids have paired ventrolateral finfolds and/or triradiate spines that have been considered as possibly homologous to either the pectoral fins (Kiaer 1924; Stensiö 1927, 1932; Robertson 1938a, 1941; Gagnier 1993b), the pelvic fins (Moy-Thomas and Miles 1971; Janvier and Arsenault 2007; Wilson et al. 2007), or both paired fins (Stensiö 1939). Homology of the paired ventrolateral finfolds of anaspids with the metapleural folds of lancelets had also been suggested (Westoll 1958; Wickstead 1969; Gagnier 1993b). Yet another hypothesis is that they represent independently derived structures (Robertson 1941; Ritchie 1964; Hopson 1974; Janvier 1987; Coates 2003). Anaspid paired fins are found in a post-branchial position and there are traces of endoskeletal supports for the finweb (Ritchie 1964; Stensiö 1964; Gagnier 1993b; Wilson et al. 2007). Some also consider that they were likely moveable structures under muscular control (Ritchie 1964; Janvier 1981b, 1984, 1987, 1996b; Wilson et al. 2007; contra Westoll, 1958). In most species, these paired fins are unconstricted and ribbon-like, with the exception of *Pharyngolepis heintzii* and *Rhyncholepis parvulus* (Ritchie 1964; Moy-Thomas and Miles 1971; Ritchie 1980; Janvier 1981b, 1984; Blom et al. 2002) where they are much shorter. The so-called pectoral spines are generally considered as forming the leading edge of the lateral finfolds (e.g., Kiaer 1924; Ritchie 1964; Moy-Thomas and Miles 1971; Ritchie 1980; Gagnier 1993b; Janvier 1996b; Blom 2008). Janvier (1996b) suggested that the posterior extent of the paired fins is constrained by the position of the anal region. Recently, it has also been found that the structure originally described as an anal fin in *Euphanerops* is in fact a paired fin (Sansom et al. 2013); paired anal fins is unique to *Euphanerops* among vertebrates. Additionally, Blom (2012) argued that the evidence in favour of the paired lateral fin-folds described for *Jamoytius* and *Euphanerops* is inconclusive, and that an alternative hypothesis is that these might actually be unpaired median structures. Based on a thorough examination of the *Euphanerops* and *Endeiolepis* material by one of us (R.C.), we confirmed the presence of paired ventrolateral finfolds in euphaneropids, as suggested by Stensiö (1939) and Janvier et al. (2007).

(8) “Thelodonti”

The stratigraphic range of the "Thelodonti" [6 orders, ~132 described species (Märss et al. 2007)] extends from the Middle Ordovician to the Upper Devonian (Märss et al. 2007). All thelodonts so far described possess a caudal fin. A dorsal fin is generally present, but can be lacking in some Thelodontiformes and Furcacaudiformes. Some authors have speculated that the epichordal lobe of at least some thelodonts could be homologous to the second dorsal fin of osteostracans and gnathostomes (Janvier 1981b; van der Brugghen 1994). An anal fin has been identified in all thelodonts where this region of the body is sufficiently well preserved, with the exception of the Furcacaudiformes where it is entirely absent (Märss et al. 2007). A possible preanal fin has been suggested for *Furcacauda fredholmae*, in the form of a rounded fin-like extension immediately anterior to the anal opening (Wilson and Caldwell 1998). Because this feature has been observed in a single specimen and that the authors expressed doubt in its interpretation as a preanal fin, we chose to score this character as unknown.

With the exception of two species of Furcacaudiformes, *Sphenonectris turnerae* and *Pezopallichthys ritchiei* (Wilson and Caldwell 1993, 1998; Märss et al. 2007), paired fins are generally present in thelodonts; however, the homology of these paired fins remains an open debate. Their insertion close to the branchial region prompted some authors to consider these paired fins as homologous to pectoral fins (e.g., Powrie 1870; Traquair 1900; Stensiö 1927; Turner 1991, 1992; Turner and Young 1992; Turner and van der Brugghen 1993; Märss and Ritchie 1998; Novitskaya and Turner 1998; Wilson and Märss 2012). Other authors have been more conservative, while still recognizing the similarity in positioning by referring to these lateral expansions as "suprabranchial fins" (Wilson et al. 2007; Johanson 2010), "pectoral flaps" (Ritchie 1968b; Dineley and Loeffler 1976; Turner 1982; Donoghue and Smith 2001; Märss et al. 2007), "pectoral swimming appendage" (Stensiö 1964), or "pectoral-level fins" (Coates 2003). Wilson

and Caldwell (1998) argued that the paired fins of traditional thelodonts (i.e. excluding the Furcacaudiformes) are inserted dorsally relative to the branchial openings making their homology to pectoral fins questionable. Another opinion is that these scale-covered lateral flaps should not be considered as "true fins" (Woodward 1900b). Moy-Thomas and Miles (1971) expressed doubt regarding the mobility of these structures and instead considered them as possibly homologous to the cornual or branchial plates of heterostracans. Alternatively, Turner (1991, 1992) suggested that the triangular flaps were likely flexible, and that the linear arrangement of scales on their surface was indicative of an underlying cartilaginous or fibrous support, thus they would not have differed from true fins at least from a functional and structural standpoint.

Among thelodonts, the Furcacaudiformes have rather unusual morphologies, which does not simplify the issue of homology with the paired fins of other agnathans. In their initial description of the group, Wilson and Caldwell (1993) stated that the ventrally positioned paired fins of furcacaudids are inserted below the branchial row and are difficult to homologize to the paired fins of other agnathans. These paired flaps extend close to the anal opening so that homology to either pectoral or pelvic fins of gnathostomes cannot be ruled out (Wilson and Caldwell 1998). Later, Wilson et al. (2007) proposed that the paired fins of most thelodonts had a suprabranchial insertion and could be precursors of pectoral fins, while the paired fins of furcacaudiforms (and of most anaspids) have a ventrolateral insertion and could be precursors of pelvic fins.

(9) “Cephalaspidomorphi”

The extinct paraphyletic "Cephalaspidomorphi" comprises the Galeaspida, Pituriaspida and Osteostraci. All of these forms are characterized by the presence of a massive cephalothoracic shield covering the head and branchial regions.

The stratigraphic range of the Galeaspida [3 orders, ~65 described species (Zhu and Gai 2007)] extends from the Lower Silurian to the Upper Devonian, with all but one localities situated in China and northern Vietnam (Janvier 1996b; Zhu and Gai 2007; Žigaitė and Blieck 2013). Galeaspids are known almost exclusively from their cephalic shields, and articulated postcranial material is rare (Janvier 1996b). So far, the trunk and caudal fin have been described only for *Sanqiaspis rostrata* (Liu 1975). To our knowledge, there was never any evidence suggesting the presence of either dorsal [although the presence of two dorsal fins has been hypothesized for *Shuyu zhejiangensis* (Gai et al. 2005; Gai et al. 2011)] or anal fins in galeaspids and most authors generally consider that they were absent (e.g., Janvier 1996a; Turner et al. 2010). There is however a small dorsal spine which is fused to the cephalic shield (Pan 1992). There is also no evidence that paired fins were present in galeaspids (Janvier 1981b, 1984; Forey and Janvier 1993; Forey 1995; Janvier 1996b, 2007; Wilson et al. 2007; Janvier 2008). No visible pectoral fin attachment areas can be seen and the postero-lateral part of the shield is generally a solid bony lobe (Janvier 1984).

Pituriaspids are known from only two species (*Pituriaspis doylei* and *Neevambaspis enigmatica*) from a single Lower-Middle Devonian locality in Queensland, Australia (Young 1991; Janvier 1996a). Only *Pituriaspis* is sufficiently well preserved to allow interpretation of its general morphology, showing an attachment area for paired fins (Young 1991). These fins can be interpreted as pectoral fins, owing to the positioning and morphology of the attachment area which is shared with osteostracans, as well as the close phylogenetic relationships between these two groups (Young 1991; Janvier 2007).

The Osteostraci [3 to 5 orders depending on recent classification, ~214 species (Janvier 1981a, 1985a, 1996b; Sansom 2008, 2009)] range from the Middle Silurian to the Upper Devonian (Sansom 2008; Žigaitė and Blieck 2013). Osteostracans are the most diverse jawless group. In all osteostracans in which the post-cephalic region is

sufficiently well known, a caudal fin is present and there are no preanal or anal fins, although many taxa do present a horizontal lobe lining the caudal fin ventrally (Heintz 1939, 1967), which some have suggested might represent a modified anal fin (Stensiö 1932, 1964; Janvier 1981b; Forey 1995; Janvier 1996a, b, 2007). Heintz (1939) considered that this horizontal lobe could not be homologized to the anal fin because the structure was distinctly paired, and that it could also not be homologized to the pelvic fins because it is inserted posteriorly to the anus; he concluded that it might be an independently derived structure. Westoll (1958) considered that the horizontal lobes of the caudal fin are posterior developments of the paired ventrolateral ridges lining the trunk (and also that the pectoral fins discussed below are anterior developments of these same ridges).

Most osteostracans have a single dorsal fin, although *Ateleaspis tessellata*, *Aceraspis robustus* and *Hirella gracilis* have anterior and posterior dorsal fins (Heintz 1939; Ritchie 1967). These species are considered as basal members of the Osteostraci (Janvier 1985c, a; Blieck and Janvier 1991; Janvier 1996b; Sansom 2008, 2009) and the presence of two dorsal fins should thus be considered as plesiomorphic for the group (Janvier 1981b). Osteostracans that have a single dorsal fin retain a series of median dorsal ridge scales along the trunk and tail (Stensiö 1932; Robertson 1935b; White 1958; Heintz 1967; Sansom 2007), and the posterior end of the cephalic shield often presents a dorsal crest and/or a dorsal spine (Robertson 1935b, a; White 1958; Heintz 1967; Adrain and Wilson 1994; Dineley 1994; Keating et al. 2012; Scott and Wilson 2012, 2013). The dorsal crest and spine of the cephalic shield have frequently been interpreted as remnants of the anterior dorsal fin found in basal osteostracans (Kiaer 1911; Stensiö 1927, 1932; Heintz 1939; Wängsjö 1952; Stensiö 1964; Heintz 1967). One hypothesis is that the dorsal crest is a modification of the cephalic shield to accommodate the reduced anterior dorsal fin which has been drawn inwards into the cephalic shield (Kiaer 1911; Heintz 1939). Another hypothesis is that the dorsal spine constitutes the anterior termination of a dorsal finfold, which is represented along the

trunk of osteostracans by the crest formed by the dorsal ridge scales (Stensiö 1932; Wängsjö 1952). As of yet, neither of these scenarios has been validated.

Pectoral fins are generally present in osteostracans, although they are lacking in the Trematapididae (Stensiö 1927, 1932; Robertson 1938a, b; Denison 1951; Moy-Thomas and Miles 1971; Halstead and Turner 1973). Trematapids being derived osteostracans, the absence of pectoral fins can be considered as a secondary loss rather than the plesiomorphic condition (Stensiö 1927; Wängsjö 1952; Stensiö 1964; Janvier 1981a, 1985c, a, b, 1996b; Sansom 2008, 2009) (contra Westoll 1945a; Denison 1951; Westoll 1958; Halstead 1982). Although the prevailing view is now that the paired fins of osteostracans are homologous to pectoral fins, this has not always been the case. Lankester (1870) hypothesized that the function of these "paired flaps" was to generate a current towards the branchial opening and that they were not involved in locomotion. Watson (1954) acknowledged the fin-like nature of these structures but considered that they were neomorphs and not homologous to the pectoral fins of gnathostomes. Concurring with Watson (1954), Janvier (Janvier 1978, 1984) argued that the paired fins of osteostracans could not be considered as homologues of the gnathostome pectoral fins because they have an epibranchial insertion, whereas pectoral fins are always post-branchial structures. Osteostracan paired fins are anteriorly positioned, there are traces of muscular attachments and foramens for the passage of nerves and blood vessels (Janvier 1978, 1996b; Johanson 2002; Janvier et al. 2004a), and there are endoskeletal supports (Janvier 1996b; Janvier and Arsenault 1996; Janvier et al. 2004a). Furthermore, the endoskeletal shoulder girdle bears a strong resemblance to that of basal gnathostomes (scapulocoracoid with a monobasal articulation for the fin endoskeletal supports), most notably when compared to the shoulder girdle of antiarchs and various other placoderms (Johanson 2002; Janvier et al. 2004a; Janvier 2007; Wilson et al. 2007). Based on these topological and structural observations, most authors agree that the paired fins of osteostracans are most likely homologous to the pectoral fins of gnathostomes (Kiaer 1924; Stensiö 1927, 1932; Wängsjö 1952; Westoll

1958; Stensiö 1964; Maisey 1986; Forey and Janvier 1993, 1994; Forey 1995; Janvier and Arsenault 1996; Johanson 2002; Janvier et al. 2004a; Janvier 2007; Sansom 2009). Other paired fins are absent although the body is triangular in cross-section and the ventral angles expand into ventrolateral keels or ridges that extend posteriorly as far as the insertion of the tail (Stensiö 1932; Heintz 1939; Westoll 1958; Stensiö 1964; Ritchie 1967; Moy-Thomas and Miles 1971; Adrain and Wilson 1994). These have been interpreted by some as remnants of ventrolateral finfolds (Kiaer 1924; Stensiö 1932; Denison 1951), or as rudimentary pelvic fins (Stensiö 1932, 1964; Moy-Thomas and Miles 1971).

(10) "Placodermi"

The fossil record of placoderms [9 orders and 335 valid genera, most of which are monospecific (Denison 1978; Young 2010)] extends from the Lower Silurian to the end of the Devonian (Young 2010; Trinajstic et al. 2014). Common to all placoderms that are sufficiently known from their postcranial anatomy is the presence of pectoral fins and a caudal fin. Conversely, an anal fin is preserved in none of these forms. There is some disparity in placoderms as to the presence of the pelvic fins and the number of dorsal fins.

Most placoderms have a single dorsal fin, although in the antiarch *Remigolepis walkeri* it is absent (Johanson 1997; Moloshnikov 2008), and ptyctodontids have two dorsal fins. The antiarch *Bothriolepis canadensi*s was originally described as having two dorsal fins (e.g., Patten 1904; Stensiö 1948), but later reexaminations of the material revealed that a single dorsal fin is actually present (Vézina 1996; Arsenault et al. 2004; Béchard et al. 2014). It is uncertain whether the most primitive placoderms (Stensioellida, Pseudopetalichthyida) had one or two dorsal fins because of the scarcity of articulated material from behind the thoracic shield (Denison 1978; Janvier 1996b). There are some debates concerning the putative presence of an anal fin in some

arthrodires: in *Coccosteus cuspidatus* and *Plourdosteus canadensis*, a ventral bony plate has been described, facing the posterior limit of the dorsal fin (Heintz 1931; Watson 1934; Vézina 1990, 1996). A possible interpretation is that it served as a basal plate supporting an anal fin (Heintz 1938; Jarvik 1960; Carr 1995; Trinajstic et al. 2014; John Long, pers. comm.). However, no traces of an anal fin web, of skeletal supports of any kind other than this plate, or of an attachment area for radials have ever been found so that other authors consider unlikely that it served as endoskeletal support for an anal fin (Heintz 1931; Westoll 1945b; Miles and Westoll 1968). Furthermore, Miles and Westoll (1968) postulated that this plate was too thin to provide support for a fin and considered instead that it most likely served as an area for an unspecified muscular attachment. Since the evidence is far from overwhelming in either case, the presence of an anal fin is dubious in *Coccosteus* and *Plourdosteus*.

Pelvic fins and/or girdles are known for most placoderm groups with the exception of petalichthyids, for which this feature has never been found, and antiarchs, where they were thought to be entirely absent (Arsenault et al. 2004; Young 2010; Zhu et al. 2012b; Trinajstic et al. 2014). As a possible exception within antiarch placoderms, pelvic flaps or fins had been suggested in *B. canadensis* (Patten 1904; Stensiö 1948; Vézina 1996), however, these structures are now considered as a taphonomic artefact (Arsenault et al. 2004; Béchard et al. 2014). Recent findings by Zhu et al. (2012b) suggest that the presence of pelvic fins might be plesiomorphic for the entire gnathostome clade, and that their absence in some placoderms is due to secondary loss, a view shared with Young (2010).

(11) “Acanthodii”

The fossil record of acanthodians, or "spiny sharks", extends as far as the Upper Silurian (Hanke 2008; Burrow and Rudkin 2014). Acanthodians comprise a little over 100 genera that have traditionally been divided into three orders: Acanthodiformes,

Climatiiformes and Ischnacanthiformes (Miles 1970; Moy-Thomas and Miles 1971; Miles 1973; Denison 1979; Zidek 1993; Zajíc 1995; Janvier 1996b; Zajíc 1998). However, many authors consider that the Diplacanthiformes constitute a fourth order closely related to the climatiiform acanthodians (e.g., Hanke et al. 2001; Hairapetian et al. 2006; Burrow and Turner 2010; Burrow and Young 2012; Newman et al. 2012; Burrow et al. 2016). Because the monophyly of the Diplacanthiformes is well supported in recent phylogenetic analyses (e.g., Hanke and Wilson 2004; Burrow and Turner 2010; Davis et al. 2012; Hanke and Davis 2012; Dupret et al. 2014; Burrow et al. 2016), we chose to retain this four order classification scheme. Furthermore, recent phylogenetic analyses support the suggestion by Gagnier & Wilson (1996) and Janvier (1996b) that at least the Climatiiformes, if not the entire Acanthodii, are paraphyletic with respect to either chondrichthyans, or both chondrichthyans and osteichthyans (Hanke and Wilson 2002, 2004; Brazeau 2009; Burrow and Turner 2010; Davis et al. 2012; Zhu et al. 2013; Brazeau and de Winter 2015; Giles et al. 2015c; Long et al. 2015; Burrow et al. 2016; Qiao et al. 2016).

Acanthodians always have caudal, anal, dorsal and pectoral fins. Median and paired fins other than the caudal are associated to spines forming the leading edge, although a fin web is not always present (Watson 1937; Moy-Thomas and Miles 1971; Denison 1979). Acanthodiforms possess a single dorsal fin, whereas climatiiforms, diplacanthiforms and ischnacanthiforms have two dorsal fins. The absence of an anterior dorsal fin is considered as a derived condition in acanthodiforms (Denison 1979; Hanke 2002; Burrow 2004). Acanthodians generally have pelvic fins, although members of the Acanthodidae lack paired pelvic fin spines (Zajíc 1995; Burrow and Young 2005; Beznosov 2009). Instead, some species have a single ventral median spine inserted close behind the pectoral fins, often bearing a long and shallow finweb (Heidtke 1990; Zajíc 1995, 1998; Beznosov 2009). Beznozov (2009) suggested a possible homology to the pelvic fin spines. However, owing to its median position and

to its insertion anteriorly to the anus, this unpaired fin spine and web found only in *Acanthodes* species was scored as a median ventral fin.

Many acanthodians also possess a series of up to six pairs of prepelvic (or intermediate) spines inserted ventrally between the pectoral and pelvic fins; prepelvic spines are generally small and only occasionally described as bearing a fin web (Watson 1937; Denison 1979; Hanke 2002; Hanke and Wilson 2006). The prepelvic fin spines may have acted as cutwaters or as defensive organs (Moy-Thomas and Miles 1971). It has also been suggested that such spines might have functioned as holdfasts in running waters (Gregory and Raven 1941), although we consider this last hypothesis unlikely. The presence of paired prepelvic spines is considered plesiomorphic for acanthodians, while their absence is derived (Watson 1937; Westoll 1945b; Westoll 1958; Moy-Thomas and Miles 1971; Denison 1979; Gagnier et al. 1999; Warren et al. 2000; Hanke 2002; Hanke and Wilson 2004). Some authors have considered the hypothesis that the prepelvic fin spines might have derived from an initially continuous lateral finfold that would have become divided and that the spines would have subsequently developed (Dean 1907; Kiaer 1924; Watson 1937; Westoll 1945b; Ørvig 1967). Others found that the prepelvic fin spines of acanthodians offer little to no support for the lateral finfold hypothesis and instead proposed that they are special developments of the ventrolateral body ridges found, for instance, in cephalaspids (Westoll 1958; Miles 1970, 1973); a hypothesis which is neither parsimonious, nor likely. Several diplacanthid and climatiid acanthodians also possess admedian spines that are positioned anteriorly to the prepelvic spines and medially to the pectoral fin spines (e.g., Watson 1937; Ørvig 1967; Denison 1979; Burrow 2007; Burrow et al. 2013; Burrow et al. 2016), and/or prepectoral spines that are generally positioned anteromedially to the pectoral fin spines (e.g., Ørvig 1967; Miles 1973; Denison 1979; Warren et al. 2000; Hanke and Davis 2008; Brazeau 2012; Hanke and Davis 2012; Newman et al. 2012; Burrow et al. 2013). Miles (1973) suggested that the pelvic, prepelvic and prepectoral fin spines formed a continuous series. Miles (1973) further hypothesized that the pectoral fins

would have initially arisen within this continuous series, but would have subsequently migrated laterally, possibly for functional reasons. Another hypothesis is that the pelvic and prepelvic spines are serial homologues (Gagnier and Wilson 1996; Hanke and Wilson 2006), whereas the prepectoral spines are serial homologues of the pectoral spines (Gagnier and Wilson 1996). As for the admedian spines, they are generally considered as the most anterior elements of the prepelvic spine series (Miles 1973; Gagnier and Wilson 1996; Hanke et al. 2001; Hanke and Davis 2008). For the purpose of this analysis, the prepelvic spines were scored as "ventrolateral paired fins," and admedian and prepectoral spines were not considered as forming separate fins.

(12) Chondrichthyes

The fossil record of Chondrichthyes [~33 orders of which 13-14 still have extant representatives; ~3000 extinct species, ~1251 extant species (Compagno et al. 2005; Klimley 2013; Nelson et al. 2016)] extends to the Lower Silurian, and possibly as far as the Upper or Middle Ordovician (Sansom et al. 1996; Young 1997; Turner 2004; Hanke and Wilson 2010; Grogan et al. 2012). Chondrichthyans include sharks, skates, rays and chimaeras and represent the most basal group of living jawed vertebrates with paired fins. They are the second most successful group of fishes still in existence today and are characterized by having a cartilaginous skeleton with prismatic endoskeletal calcification, and by males possessing modified myxopterygia, termed claspers, used for internal fertilization (Schaeffer and Williams 1977; Schaeffer 1981; Maisey 1984a; Maisey 1986; Grogan and Lund 2004; Grogan et al. 2012). Two main evolutionary lineages are recognized, the Euchondrocephali and the Elasmobranchii, which have been traditionally considered as sister groups (Schaeffer and Williams 1977; Lund and Grogan 1997; Grogan and Lund 2004; Lund and Grogan 2004; Grogan et al. 2012). This scenario is supported by most phylogenetic analyses (e.g., Lund and Grogan 1997; Grogan and Lund 2000, 2004; Grogan and Lund 2008; Inoue et al. 2010), although the Euchondrocephali have been found occasionally to be nested within a paraphyletic

assemblage of elasmobranchs (e.g., Coates and Sequeira 2001a, b; Ginter et al. 2010). Furthermore, the phylogenetic position of the Iniopterygii, a clade of peculiar-looking fishes with enlarged pectoral fins that are inserted high along the side of the body (Zangerl and Case 1973; Zangerl 1997; Grogan and Lund 2009), is unclear. The iniopterygians are either considered to be nested within the Euchondrocephali (Lund and Grogan 1997; Grogan and Lund 2000, 2004), or they represent basal chondrichthyans placed stemward to the Euchondrocephali-Elasmobranchii split (Grogan and Lund 2009; Grogan et al. 2012; Lund et al. 2014).

The Euchondrocephali include 12 orders among which only the Chimaeriformes contain extant species. They have a fossil record which extends to the Lower Carboniferous (Lund and Grogan 1997; Grogan and Lund 2004; Grogan et al. 2012). The more advanced forms, the Holocephali, are characterized by the presence of an erectile first dorsal fin spine that articulates, via a basal plate, with the dorsal process of the synarcual, a structure formed from the fusion of the anteriormost vertebrae (Maisey 1986; Didier 1995; Didier et al. 2012). The disparity in fin configurations observed in the Euchondrocephali results mostly from the dorsal fin which can be present, either as a single fin or as two separate fins, or absent, and the presence/absence of the anal fin. The evidence as to the plesiomorphic number of dorsal fins in chondrichthyans is inconclusive. Lund (1985) wrote that arguments of equal weight could be made for the presence of a single dorsal fin, as in Xenacanthiformes, *Heteropetalus* and Chondrenchelyiformes, or two dorsal fins as in *Cladoselache*. Lund and Grogan (1997) later mentioned that the accumulated evidence seemed to support the elongation of the second dorsal fin into the single fin found in these taxa as a derived condition. The Euchondrocephali also include the Eugeneodontiformes, which is the only chondrichthyan order showing the loss of the pelvic fins.

The stem Elasmobranchii comprise nine orders, but only four of these are represented by complete articulated postcranial material. Caudal, pectoral and pelvic fins are

always present in these forms that range from the Devonian to the Cretaceous. There is some disparity as to the number of dorsal fins and the presence/absence of the anal fin. Additionally, the dorsal fin is described as entirely lacking in *Thrinacodus* (= *Thrinacoselache*) *gracia* (Phoebodontiformes) (Grogan and Lund 2008; Ginter and Turner 2010).

The crown group Elasmobranchii are the Neoselachii, which include the Selachii and the Batoidea. The Neoselachii have a fossil record that extends to the Lower Jurassic (Maisey 1984b; Grogan et al. 2012; Maisey 2012). The Selachii, or modern sharks, are fairly homogeneous in terms of fin configurations. As with stem Elasmobranchii, the caudal, pectoral and pelvic fins are always present. There are generally two dorsal fins, but there is a single dorsal fin in Hexanchiformes, and in some species of Synechodontiformes and Carcharhiniformes. The anal fin is present in most orders, although it is generally absent in the Squalomorphi (i.e. an anal fin is absent in Squaliformes, Protospinaciformes, Pristiophoriformes and Squatiniformes, but is present in Hexanchiformes), a condition which is considered as derived relatively to other neoselachians (Compagno 1977).

Batoids comprise four orders that include about 630 species, representing about half of extant chondrichthyan biodiversity (Aschliman et al. 2012a). The fossil record of batoids extends to the Lower Jurassic (Maisey 2012). Batoids possess highly derived paired fin morphologies and are much more disparate in their fin configurations than the Selachii. Again, the pectoral and pelvic fins are always present in batoids. The pectoral fins are connected to the antorbital process of the cranium and are generally greatly enlarged to the point of frequently being referred to as wings (Rosenberger 2001; Schaefer and Summers 2005; Franklin et al. 2014). The number of dorsal fins differs among species: it can be absent, and when present there can be one or two dorsal fins. The anal fin is also frequently absent, and in many species of Rajiformes and Myliobatiformes, the tail is long and whip-like and devoid of a terminal caudal web.

Some issues warrant supplementary explanations as to how we scored fin characters among batoids. In Myliobatiformes, some species bear spines or barbs with a dorsal insertion along the tail: there are generally one or two spines, occasionally three, and rarely four or five (Halstead 1978; Thorson et al. 1988; Amesbury and Snelson 1997; Lowe et al. 2007). These spines are composed of a vitrodentine core with an external layer of enameloid and are anchored in a dense collagenous network of the dermis on the dorsal side of the caudal appendage (Halstead et al. 1955; Halstead 1978; Amesbury and Snelson 1997; Johansson et al. 2004). These caudal spines are thought to be modified placoid scales (Reif 1982; Kemp 1999; Johansson et al. 2004), and as such, they were not scored as fins. Another issue concerning some Myliobatiformes pertains to the rostral or cephalic fins (Jordan and Evermann 1896; Smith 1907; Garman 1913; Fowler 1941; Tinker 1944; Bigelow and Schroeder 1953). These are extensions of the pectoral fins, which are interrupted on the sides of the head and reappear in front of the snout as fleshy protuberances (Garman 1913; Meek and Hildebrand 1923; Mulvany and Motta 2013). Additionally, a number of batoid taxa are also described as having lateral keels or ridges along the tail (e.g., Bean and Weed 1909a, b; Bigelow and Schroeder 1958). These were not scored as unconstricted paired fins owing to their location along the tail, behind the insertion of the pectoral and pelvic fins.

A final source of disparity in fin configuration should be mentioned as it relates to the "total group chondrichthyans." This disparity concerns the presence of prepelvic fin spines between the pectoral and pelvic fins in at least two putative chondrichthyans, *Kathemacanthus rosulentus* and *Seretolepis elegans* (Gagnier and Wilson 1996; Hanke and Wilson 2010). If acanthodians are added to the total group chondrichthyans as suggested by recent investigations (e.g., Brazeau and de Winter 2015; Giles et al. 2015c; Long et al. 2015; Burrow et al. 2016; Qiao et al. 2016), the presence of prepelvic spines will become a common character of stem chondrichthyans.

(13) Actinopterygii

Among fishes, actinopterygians, or ray-finned fishes, have achieved a remarkable ecological and evolutionary success (Lauder and Liem 1983), resulting in over 30 500 species (Nelson et al. 2016), as well as an abundant fossil record extending to the Upper Silurian (Cloutier and Arratia 2004). The diversity of actinopterygians represents close to half of all described vertebrate species. Not only are actinopterygians impressively species-rich, but they are also extremely morphologically disparate, and part of this disparity can readily be observed in differences in fin configurations. Indeed, many changes in modes of feeding and locomotion are associated with modifications of the structure, size, number and position of fins (Webb 1982; Lauder and Liem 1983; Webb 1984; Lauder and Drucker 2004).

Basal actinopterygians comprise two extant orders [Polypteriformes (bichirs and reedfishes) and Acipenseriformes (sturgeons and paddlefishes)] and about ten extinct orders of fishes. The presence of a single dorsal fin has been considered as an actinopterygian synapomorphy (Cloutier and Arratia 2004). *Dialipina salgueiroensis*, one of the oldest putative actinopterygians from the Lower Devonian, has two dorsal fins (Schultze and Cumbaa 2001). However, since its description, phylogenetic investigations have placed *Dialipina* sometimes as a stem actinopterygian (Taverne 1997; Schultze and Cumbaa 2001; Zhu and Schultze 2001; Zhu et al. 2006; Zhu et al. 2009; Giles et al. 2015b; Long et al. 2015), and other times as a stem osteichthyan (Friedman 2007; Brazeau 2009; Davis et al. 2012; Dupret et al. 2014; Brazeau and de Winter 2015; Giles et al. 2015c; Burrow et al. 2016; Lu et al. 2016a; Qiao et al. 2016). Other basal actinopterygians have a single dorsal fin, a single anal fin, a caudal fin and pectoral fins. The pelvic fins are sometimes lacking in a few species of Polypteriformes, "Palaeonisciformes" and Tarrasiiformes.

Basal neopterygians include two extant orders [Lepisosteiformes (gars) and Amiiformes (bowfins)] as well as a dozen extinct orders. Their fin configurations resemble those of basal actinopterygians although to our knowledge, the loss of the pelvic fins has not been observed in any of the described taxa. However, a second dorsal fin has been described for the genera *Placidichthys*, which belongs to the extinct order Ionoscopiformes (Brito 2000; Brito and Alvarado-Ortega 2008).

Basal teleosteans are extremely diversified and include a number of very speciose marine and freshwater groups: notably the Osteoglossomorpha, Elopomorpha, Clupeomorpha and Ostariophysy. Among the Osteoglossomorpha (bony-tongues and their allies), the Osteoglossiformes comprises species that use a mode of locomotion based on undulations of the anal fin (Notopteridae), or of the dorsal fin in the case of the monotypic family Gymnarchidae (McNeill Alexander 1967; Lindsey 1978). The fin that is used for propulsion is elongated in these forms, and in some species the pelvic, dorsal, anal and/or caudal fins can be lost.

The Elopomorpha (eels and their allies) are mostly fishes with an elongated body shape, and many species have developed an anguilliform mode of locomotion whereby the entire body is used in undulations that produce thrust (Webb 1975; Lindsey 1978; Sfakiotakis et al. 1999). As such, the dorsal and anal fins are often well developed and continuous with the caudal fin, while the paired fins are reduced or lost. The most disparate elopomorphs in terms of fin configurations belong to the order Anguilliformes. In Anguilliformes, the pelvic fins are always absent and in many species, the pectoral fins are lost as well. Additionally, the median fins are frequently reduced to some extent or lost, and in some taxa, fins are entirely lacking in the adult (McCosker 1977, 2004).

The Clupeomorpha (sardines and their allies) are comparatively far less disparate. The pelvic fins are frequently lost, and the reduction or loss of the dorsal fin is described

for at least one specie, *Raconda russeliana* (Gray 1831). Furthermore, in species of *Sundasalanx*, a median ventral finfold is present, positioned between the pelvic and anal fins (Roberts 1981; Siebert 1997).

The Ostariophysi are extremely species-rich and are generally the group best represented in freshwater piscine communities. Ostariophysans correspondingly present very disparate fin configurations, particularly in the Siluriformes (catfishes), and to a lesser extent in the Gymnotiformes (knifefishes and their allies). In Siluriformes, loss of the dorsal, anal and/or pelvic fins is observed in many species. In the Eel catfish, *Channallabes apus*, the presence of the pectoral and pelvic fins varies intraspecifically: in some specimens, both paired fins are present, in others both paired fins are absent, and yet in others only the pectoral fins are present (Adriaens et al. 2002). In members of the Plotosidae, there is a second ray-supported dorsal fin which is confluent with the caudal and anal fins (Jayaram 1981, 1982; Gormon 1986; Ferraris 1999; Nelson et al. 2016); it seems likely that this second dorsal fin is supported by a series of anteriorly expanding and enlarged upper procurrent rays of the caudal fin (Gormon 1986; Allen 1998; Ferraris 1999). Members of the Gymnotiformes use an anal fin based mode of locomotion (McNeill Alexander 1967; Webb 1975; Lindsey 1978; Sfakiotakis et al. 1999; de Santana et al. 2013), as with the previously mentioned Notopteridae. These two groups are not closely related (Alves-Gomes 1999; Lavoué et al. 2012; Near et al. 2012), thus their similarities in terms of body shape and anal fin based propulsion have been independently acquired. Pelvic fins and a ray-supported dorsal fin have been lost in all Gymnotiformes, and the caudal fin is absent in four of the five families of this order.

Another source of disparity in ostariophysan fin configurations is the presence/absence of the adipose fin, which is usually a small, primitively non-rayed fin located medially between the dorsal and caudal fins (Reimchen and Temple 2004; Buckland-Nicks et al. 2012; Stewart 2015; Aiello et al. 2016). The adipose fin first appears among the

Ostariophysii (Characiformes and Siluriformes), but it is also found in several orders of more advanced Euteleostei (Argentiniformes, Salmoniformes and Osmeriformes) and Neoteleostei (Stomiiformes, Ateleopodiformes, Aulopiformes, Myctophiformes and Percopsiformes). These orders do not constitute a natural group, suggesting that the adipose fin might have evolved multiple times independently (Stewart et al. 2014; Stewart 2015), or that it was subsequently lost in some groups (Esociformes, Lampridiformes). The adipose fin was hypothesized to be a degenerate appendage homologous to the posterior dorsal fin of basal gnathostomes (Bridge 1904; Garstang 1931). Later investigations suggested instead that the rudimentary appearance of the adipose fin is plesiomorphic (Sandon 1956; Stewart and Hale 2013; Stewart et al. 2014). In some euteleosteans, there is also a median ventral keel or finfold, often termed a ventral adipose fin, which is positioned anteriorly to the anal fin: this ventral fin has been described in some Osmeriformes, Stomiiformes, Aulopiformes and Gasterosteiformes (Greenwood et al. 1966; Fischer and Bianchi 1984; Froese and Pauly 2016; Nelson et al. 2016) and was scored as a median ventral fin in our dataset. In the Apteronotidae, a fleshy dorsal electroreceptive organ (also called "dorsal filament" or "dorsal thong") is present. Some have suggested that it might constitute a modified adipose fin (Kaup 1856; Boulenger 1898). The dorsal organ of apteronotids and the adipose fins of other ostariophysans share a similar location along the dorsal midline, and are both scaleless and composed principally of connective tissues and sense organs (Franchina and Hopkins 1996). Despite these similarities, Franchina and Hopkins (1996) found that the hypothesis of an evolutionary modification of the adipose fin and the hypothesis of an evolutionary novelty should be considered as equally parsimonious. An elongated adipose fin has also been described for a single fossil representative of the Gymnotiformes, *Humboltichthys kirschbaumi*, although the authors acknowledged that it corresponds topologically to the apteronotid dorsal electroreceptive organ (Gayet and Meunier 1991; Gayet et al. 1994). Furthermore, it has been argued that the hypothesized adipose fin in *Humboltichthys* could be a

taphonomic artefact due to compression of the body outline (Albert 2001; Albert and Fink 2007).

The more advanced teleosteans are the Euteleostei and the Neoteleostei. In addition to the dorsal and ventral adipose fins, the most notable source of disparity in fin configurations among the orders of basal euteleosteans and neoteleosteans is the occasional absence of the pelvic fins. Among the Stomiidae, the pectoral fins are absent in adults of *Photostomias*, *Idiacanthus* and *Tactostoma* (Bolin 1939; Kawaguchi and Moser 1984; Fink 1985; Goodyear and Gibbs 1986; Hulley 1986; Kenaley and Hartel 2005). Additionally, in the sexually dimorphic genus *Idiacanthus*, adult females only lack the pectoral fins, whereas males lack both pectoral and pelvic fins (Hulley 1986).

The more advanced Neoteleostei are the Acanthomorpha, which include the extremely species-rich Acanthopterygii. Acanthomorphs are characterized by the presence of spines in their dorsal and anal fins (Johnson and Patterson 1993). A major source of disparity in fin configurations among acanthomorphs concerns the median fins: there are frequently two separate dorsal or anal fins, and even occasionally a third dorsal fin, for instance in some Gadiformes (cods and their allies). The loss of fins also remains as an important source of disparity in fin configurations in acanthomorphs. All of the median and paired fins can be lost, including the caudal fin in at least some species of six orders. Finally, in some groups, fins can be co-opted to serve novel functions. Examples include the co-option of the first dorsal fin into a fishing apparatus (spines of the plesiomorphic spinous dorsal fin are modified into an illicium which serves as the rod, and an esca which is the bait) in anglerfishes (Lophiiformes) (Lauder and Liem 1983; Pietsch 1984; Pietsch and Orr 2007) or into a suctorial apparatus in remoras (Echeneidae, Perciformes) (Storms 1888; O'Toole 2002; Fulcher and Motta 2006; Britz and Johnson 2012; Friedman et al. 2013a), or the co-option of the pelvic fins into a suctorial organ in lumpsuckers and snailfishes (Cyclopteridae and Liparidae

respectively, both belong to Scorpaeniformes) (Gill 1890; Budney and Hall 2010; Voskoboinikova and Kudryavtseva 2014).

(14) Sarcopterygii

Sarcopterygians are a monophyletic group that includes lobe-finned fishes as well as all tetrapods (Schultze 1986, 1993; Cloutier and Ahlberg 1996; Janvier 1996b). They are characterized by paired fins that are supported by a monobasal endoskeleton (Cloutier and Ahlberg 1996; Janvier 1996b). For the purpose of this review, we will focus on the piscine sarcopterygians [7 orders; 8 extant species; ~190 extinct genera (updated from Cloutier and Ahlberg 1996)], which comprise only a few extant species but are nonetheless represented by a diversified fossil record extending as far as the Late Silurian (Zhu and Schultze 1997). The recent discovery of nearly complete basal sarcopterygians, such as *Guiyu* and *Psarolepis*, provide some potential insight into the plesiomorphic condition for the group (Yu 1998; Zhu et al. 1999; Zhu et al. 2006; Zhu et al. 2012a).

Basal sarcopterygians include the Onychodontiformes and the Actinistia. Onychodontiformes are known from only six genera and their fossil record extends from the Lower to the Upper Devonian (Cloutier and Ahlberg 1996; Lu and Zhu 2010; Lu et al. 2016b). Postcranial material is known only for a few species: they all have pectoral and pelvic fins, two dorsal fins, a single anal fin, and a caudal fin (Jessen 1966; Andrews et al. 2005). Actinistians, or coelacanths, are known from two extant species and their fossil record extends from the Lower Devonian to the Upper Cretaceous (Cloutier and Ahlberg 1996; Forey 1998; Johanson et al. 2006; Friedman 2007; Arratia and Schultze 2015). Actinistians display little disparity in fin configurations, even in terms of the shape of individual fins with a few rare exceptions concerning caudal fin morphology (Cloutier 1991; Forey 1998; Wendruff and Wilson 2012). The generalized fin configuration observed in the living *Latimeria* species is considered to be an

example of conservative evolution, because it does not differ importantly from the fin configuration found in Carboniferous actinistians (Cloutier 1991). Most actinistians typically have a triphycercal caudal fin that consists of symmetrical dorsal and ventral lobes separated by a smaller supplementary lobe, which differs in size among species. However, some species have highly asymmetrical caudal fins where either the epichordal (e.g., *Allenypterus*; *Piveteauia*) or the hypochordal lobes (e.g., *Miguashaia*) are more developed (Cloutier 1991; Forey 1998). Uyeno (1991) suggested that what is considered as a trilobed caudal fin in *Latimeria* is actually a third dorsal and a second anal fin in which the rays are borne on pterygiophores, and these flank a small true caudal fin with rays unsupported by pterygiophores. However, this hypothesis has never been validated. Actinistians are also characterized by the structural similarities between the endoskeleton of dorsal and anal fins, and that of the paired fins (Schultze 1986; Forey 1998).

The Dipnomorpha include the Porolepiformes and the Dipnoiformes. The fossil record of porolepiforms includes about eight genera and extends from the Lower to the Upper Devonian (Cloutier and Ahlberg 1996; Janvier 1996b), although a possible Early Carboniferous occurrence has been recorded (Schultze 1993). All porolepiforms have pectoral and pelvic fins, two dorsal fins, a single anal fin and a caudal fin. Porolepiforms are characterized as having widely differing paired fin morphologies: the pectoral fins are long, leaf-like and asymmetrical while the pelvic fins are shorter, rounded and asymmetrical (Ahlberg 1989). Furthermore, in *Quebecius quebecensis*, only the pectoral fins are lobed, whereas the pelvic fins are not (Cloutier and Schultze 1996). The Dipnoiformes, or lungfishes, include six living species and at least 81 genera with a fossil record extending to the Lower Devonian (Cloutier and Ahlberg 1996). All dipnoans have lobed pectoral and pelvic fins, but there is some disparity in the configuration of the median fins, which creates difficulties in the interpretation of dorsal, anal and caudal fin characters. Early Devonian dipnoans have two dorsal fins, which is considered as the plesiomorphic condition for the group (Schultze 1986). The

more derived dipnoans possess a single median fin that is continuous around the tail (Friedman 2010), and the caudal fin has changed from heterocercal to diphycercal (Johanson et al. 2009). Friedman (2010) reviewed the evolutionary scenarios that have been proposed to explain the emergence of this continuous median fin in derived dipnoans, which he summarized as either: (1) reversal to a hypothetical ancestral protocercal condition (Goodrich 1930; Bemis 1984); (2) loss of the caudal and posterior expansion of the dorsal and anal fins (Balfour and Parker 1882; Abel 1911; Arratia et al. 2001); (3) loss of dorsal and anal fins and anterior expansion of the caudal fin (Schmalhausen 1913); (4) expansion of the plesiomorphic two narrow dorsal fins that fuse with the epichordal lobe of the caudal fin and loss of the anal fin (Dollo 1895); (5) or consolidation of the dorsal, anal and caudal fins (Westoll 1949; Arratia et al. 2001; Long and Clement 2009). Friedman (2010) concluded that hypotheses 1 through 3 were improbable, and argued that out of the two remaining hypotheses, the prevalence of a regionalized endoskeleton supporting the hypochordal lobe favored incorporation of the anal fin rather than its loss. Contrastingly, in a detailed study of the ontogeny of *Neoceratodus forsteri*, Johanson et al. (2009) found better support for hypothesis 4. These authors suggest that the dorsal part of the diphycercal fin of Carboniferous and extant lungfishes is formed by the confluence of the two dorsal fins found in more basal members with the epichordal lobe of the caudal fin, whereas the ventral part of the fin is formed only by the hypochordal lobe, and the anal fin is lost entirely (Johanson et al. 2009).

The piscine Tetrapodomorpha include the Rhizodontiformes, "Osteolepiformes" and "Elpistostegalia." Rhizodontiformes range from the Upper Devonian to the Lower Carboniferous, while "Osteolepiformes" range from the lower Middle Devonian to the Lower Permian (Cloutier and Ahlberg 1996; Janvier 1996b). Rhizodontiforms and osteolepiforms present the fin combinations characteristic of most sarcopterygian taxa: presence of pectoral and pelvic fins, two dorsal fins, a single anal fin and a caudal fin. The paraphyletic elpistostegalians include the closest relatives to tetrapods and their

fossil record extends from the Middle to Upper Devonian (Cloutier and Ahlberg 1995; Cloutier and Ahlberg 1996; Daeschler et al. 2006; Swartz 2012). They are a poorly documented group and in the few taxa where postcranial material is preserved, median fins are no longer present (R.C., pers. observ.) with the exception of the caudal fin, while the paired fins are composed of robust endochondral elements, some of which can be homologized to those found in tetrapod limbs (Vorobyeva and Schultze 1991; Vorobyeva and Hinchliffe 1996; Hinchliffe et al. 2001; Boisvert 2005; Shubin et al. 2006; Boisvert et al. 2008; Shubin et al. 2014).

ANNEXE C

LIST OF SOURCE TREES FOR THE SUPERTREE ANALYSIS AND ADDITIONAL RESULTS

Table C1: List of source trees that were incorporated into the MRP supertree analyses.

Tree sections	Published phylogenies
Agnathans	(Janvier 1996a; Donoghue et al. 2000; Donoghue and Smith 2001; Holland and Chen 2001; Hou et al. 2002; Shu et al. 2003a; Wilson and Märss 2004; Sansom et al. 2005; Gess et al. 2006; Wilson and Märss 2009; Sansom et al. 2010; Turner et al. 2010; Blom 2012; Morris and Caron 2014; Keating and Donoghue 2016; McCoy et al. 2016)
Placoderms and Acanthodians	(Forey and Gardiner 1986; Hanke and Wilson 2004; Brazeau 2009; Carr et al. 2009; Burrow and Turner 2010; Davis et al. 2012; Hanke and Davis 2012; Zhu et al. 2013; Dupret et al. 2014; Giles et al. 2015a; Giles et al. 2015c; Long et al. 2015; Burrow et al. 2016; Lu et al. 2016a)
Chondrichthyans	(Dunn and Morrissey 1995; de Carvalho and Maisey 1996; Kitamura et al. 1996; Shirai 1996; Lund and Grogan 1997; Grogan and Lund 2000; Sequeira and Coates 2000; Coates and Sequeira 2001b; Douady et al. 2003; Grogan and Lund 2004; Winchell et al. 2004; Naylor et al. 2005; Dosay-Akbulut 2006; Human et al. 2006; Grogan and Lund 2008; Inoue et al. 2010; Klug 2010; Vélez-Zuazo and Agnarsson 2011; Aschliman et al. 2012a; Aschliman et al. 2012b; Li et al. 2012; Naylor et al. 2012; Lund et al. 2014; Pavan-Kumar et al. 2014)
Actinopterygians	(Gardiner and Schaeffer 1989; Johnson and Patterson 1993; Le et al. 1993; Grande and Bemis 1998; Arratia 1999; Coates 1999; Arratia 2000; Wiley et al. 2000; Filleul and Lavoué 2001; Inoue et al. 2001; Schultze and Cumbaa 2001; Inoue et al. 2003; Ishiguro et al. 2003; Saitoh et al. 2003; Inoue et al. 2004; Gardiner et al. 2005; Lavoué et al. 2005; Miya et al. 2005; Cavin and Suteethorn 2006; Hurley et al. 2007; Arratia 2008; Kawahara et al. 2008; Setiamarga et al. 2008; Inoue et al. 2009;

Tree sections	Published phylogenies
	Li et al. 2009; Cavin 2010; López-Arbarello 2012; Near et al. 2012; Betancur-R et al. 2013; Broughton et al. 2013; Faircloth et al. 2013; Miya et al. 2013; Near et al. 2013; Dornburg et al. 2014; Delbarre et al. 2015; Eytan et al. 2015; Xu et al. 2015; Arratia 2016)
Sarcopterygians	(Ahlberg 1991; Young et al. 1992; Cloutier and Ahlberg 1996; Chang and Yu 1997; Zhu and Schultze 1997; Ahlberg and Johanson 1998; Zhu et al. 1999; Johanson and Ahlberg 2001; Zhu and Schultze 2001; Zhu et al. 2001; Coates et al. 2002; Zhu and Yu 2002; Zhu and Ahlberg 2004; Daeschler et al. 2006; Long et al. 2006; Friedman 2007; Friedman et al. 2007; Snitting 2008; Holland and Long 2009; Zhu et al. 2009; Lu et al. 2012; Swartz 2012; Lu et al. 2016b)

Figure C1: 50% majority rule consensus of the supertrees obtained using Nixon's parsimony ratchet.

Figure C2: Strict consensus of the supertrees obtained using Nixon's parsimony ratchet.

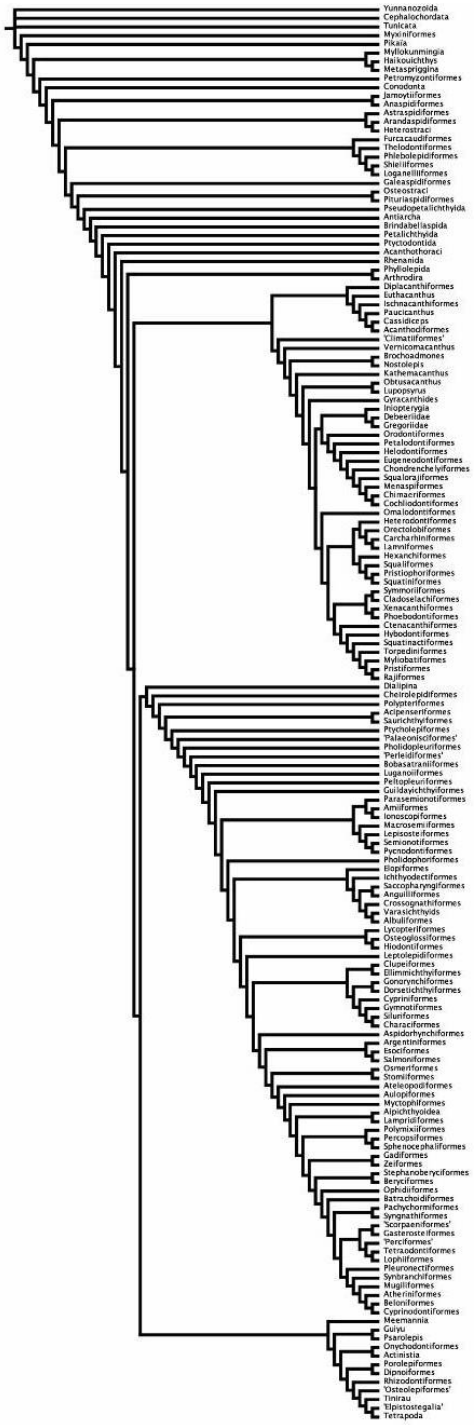


Figure C3: Supertree obtained using optimum parsimony.

Insights of the supertree into basal vertebrate interrelationships

The phylogenetic relationships of basal vertebrates have not yet reached a stable consensus. Four groups that have been strongly debated concerning their interrelationships to other fishes are the conodonts, the extant agnathans (hagfishes and lampreys), the placoderms and the acanthodians. The consensus topology from our supertree considers cyclostomes, acanthodians and placoderms as paraphyletic groups. Furthermore, the supertree places conodonts within vertebrates, placoderms as stem gnathostomes, and acanthodians as stem chondrichthyans.

Conodont interrelationships have been vigorously debated, the two prevailing views being that they are either stem chordates (Aldridge et al. 1986; Aldridge 1987; Aldridge and Briggs 1990; Pridmore et al. 1997; Blieck et al. 2010; Turner et al. 2010), or that they are stem craniates or even stem vertebrates (Briggs 1992; Aldridge and Theron 1993; Briggs and Kear 1994; Gabbott et al. 1995; Purnell 1995; Aldridge and Purnell 1996; Donoghue et al. 1998; Donoghue et al. 2000; Sweet and Donoghue 2001; Schubert et al. 2006). Morphological arguments that have been used to promote the craniate or vertebrate hypotheses include the presence of a ray-supported caudal fin, eyes with extrinsic musculature and paired sensory structures that are interpreted as indirect evidence of a brain (Gabbott et al. 1995; Aldridge and Purnell 1996; Donoghue et al. 1998; Donoghue et al. 2000; Sweet and Donoghue 2001; Janvier 2007). Arguments against the vertebrate interpretation of conodonts include that cephalisation is low in conodonts, that their trunk musculature is V-shaped rather than W-shaped, and that they lack dermal fin rays supporting the fins, a gill basket and a dermal skeleton (Blieck et al. 2010; Turner et al. 2010). Additionally, based on histological investigations, some authors have hypothesized that conodonts possess vertebrate-like hard tissues in the form of globular calcified cartilage, cellular bone, an enamel-homologue and dentine (Briggs 1992; Sansom et al. 1992; Sansom et al. 1994; Smith et al. 1996), but these findings have been met with criticisms (Kemp and Nicoll 1995;

Kemp and Nicoll 1996; Schultze 1996; Kemp 2002b, a; Reif 2006; Blieck et al. 2010; Turner et al. 2010). Ultimately, the position of conodonts in phylogenies results largely from how some of the homologies are interpreted (Janvier 2003; Turner et al. 2010). Although the conodont fossil record is extremely abundant, it mostly consists of elements of the oral apparatus and only a few articulated specimens with postcranial material have been discovered. As with the cyclostomes, the debate over conodont interrelationships remains an open question and will probably remain so until further well-preserved material is unraveled.

Two competing hypotheses have been proposed concerning the interrelationships of extant agnathans and gnathostomes: (1) either lampreys and hagfishes form a clade called the cyclostomes (Duméril 1806; Schaeffer and Thomson 1980; Shimeld and Donoghue 2012), (2) or hagfishes are craniates while lampreys are vertebrates, making the "cyclostomes" paraphyletic relative to gnathostomes (Løvtrup 1977; Janvier 1978; Dingerkus 1979; Hardisty 1979; Janvier and Blieck 1979; Janvier 1981b; Forey 1984; Jefferies 1986; Forey and Janvier 1993; Janvier 1996b). Although cyclostome monophyly was initially proposed based on morphological arguments (e.g., Schaeffer and Thomson 1980; Yalden 1985), more recently it has been advocated mainly on the grounds of molecular phylogenetic analyses (e.g., Stock and Whitt 1992; Mallatt and Sullivan 1998; Hedges 2001; Mallatt et al. 2001; Delarbre et al. 2002; Heimberg et al. 2010), whereas the analyses based on morphological datasets and incorporating fossil taxa have generally resolved hagfishes and lampreys as paraphyletic relative to gnathostomes (Forey 1995; Janvier 1996a; Donoghue et al. 2000; Donoghue and Smith 2001; Gess et al. 2006; Khonsari et al. 2009; Turner et al. 2010; Miyashita 2012). Although our consensus topology considers the cyclostomes as paraphyletic, the debate seems far from settled as both hypotheses are difficult to reconcile on the grounds of both morphological and molecular evolution. However, cyclostome monophyly implies either that lampreys and gnathostomes share an impressive amount of homoplastic characters, or that there is a no-less impressive history of reversals among

hagfish characters (Delarbre et al. 2002; Janvier 2007; Heimberg et al. 2010). We agree with the opinion that cyclostome monophyly cannot be resolved on the basis of molecular data alone and requires the incorporation of evidence from the fossil record (Miyashita 2012; Abou Chakra et al. 2014).

For many years, placoderms and acanthodians were considered by most to be monophyletic groups: placoderms were considered as the sister group to crown gnathostomes (Schaeffer and Williams 1977; Goujet and Young 2004), while acanthodians were considered as a clade of stem osteichthyans (Moy-Thomas and Miles 1971; Schaeffer and Williams 1977; Denison 1979). Although some studies have focused on intra-relationships within placoderms (Forey and Gardiner 1986; Goujet and Young 1995; Goujet and Young 2004; Carr et al. 2009) or acanthodians (Hanke and Wilson 2004; Burrow and Turner 2010; Hanke and Davis 2012), recent matrix-based analyses at a larger phylogenetic scale do not support the monophyly of either of these groups. The accumulated evidence now seems to support the prevailing view that placoderms are paraphyletic stem gnathostomes, while acanthodians are either paraphyletic stem chondrichthyans (Zhu et al. 2013; Brazeau and de Winter 2015; Giles et al. 2015c; Long et al. 2015; Burrow et al. 2016; Qiao et al. 2016), or even polyphyletic, with some taxa as stem gnathostomes, others as stem chondrichthyans and yet others as stem osteichthyans (Brazeau 2009; Davis et al. 2012). A single recent analysis has resolved acanthodians as the monophyletic sister group of chondrichthyans (Dupret et al. 2014). Importantly, all of these recent phylogenetic analyses that have focused on the interrelationships of placoderms, acanthodians and gnathostomes used modified data matrices from Brazeau (2009). In some of these analyses, it has been observed that the addition or exclusion of taxa and/or characters reveal conflicting signals within the dataset as well as unstable topologies (Davis et al. 2012; Brazeau and Friedman 2015). Our consensus supertree results in a topology where placoderms are paraphyletic stem gnathostomes and acanthodians are paraphyletic stem chondrichthyans, although we realize that this reflects the most

common findings based on multiple analyses that are not independent from one another. We conclude that the monophyly of these groups is unlikely, but cannot be entirely rejected. Lists of characters have been proposed as supporting the monophyly of both placoderms (Goujet and Young 2004; Young 2008, 2010) and acanthodians (Burrow and Turner 2010).

ANNEXE D

PRESENCE/ABSENCE DATASET

Group;Order;MVF;UPF;PECT;PELV;DORS;ADIP;ANAL;CAUD

Deuterostomes;Yunnanozoida;1;1;0;0;1;0;0;NA

Deuterostomes;Yunnanozoida;1;0;0;0;1;0;0;1

Deuterostomes;Incertae_sedis;1;0;0;0;1;0;0;0

Cephalochordata;Incertae_sedis;0;0;0;0;0;0;0;0

Cephalochordata;Amphioxiformes;1;0;0;0;1;0;0;1

Tunicata;Appendicularia;0;0;0;0;0;0;0;1

Tunicata;Ascidia_thalia;0;0;0;0;0;0;0;0

Stem_vertebrata;Incertae_sedis;NA;0;0;0;0;0;0;0

Stem_vertebrata;Myllokunmingiida;1;0;0;0;1;0;0;1

Myxini;Myxiniformes;1;0;0;0;1;0;0;1

Myxini;Myxiniformes;0;0;0;0;0;0;0;0

Myxini;Myxiniformes;1;0;0;0;0;0;0;1

Myxini;Myxiniformes;0;0;0;0;0;0;0;1

Myxini;Myxiniformes;1;1;0;0;0;0;0;1

Petromyzontida;Petromyzontiformes;0;0;0;0;1;0;0;0

Petromyzontida;Petromyzontiformes;0;0;0;0;1;0;0;1

Petromyzontida;Petromyzontiformes;0;0;0;0;2;0;0;1

Petromyzontida;Petromyzontiformes;0;0;0;0;2;0;1;1

Petromyzontida;Petromyzontiformes;0;0;0;0;1;0;1;1

Conodonta;Ozarkodinida;0;0;0;0;1;0;0;1

Conodonta;Ozarkodinida;0;0;0;0;0;0;0;1

Pteraspidomorphi;Astraspida;0;0;0;0;0;0;0;1

Pteraspidomorphi;Arandaspida;0;0;0;0;0;0;0;1

Heterostraci;Cyathaspidiformes;0;0;0;0;0;0;0;1

Heterostraci;Pteraspidiformes;0;0;0;0;0;0;0;1
Anaspida;Jamoytiiformes;0;0;0;0;1;0;1;1
Anaspida;Jamoytiiformes;0;0;0;0;0;0;1;1
Anaspida;Jamoytiiformes;0;1;0;0;1;0;1;1
Anaspida;Anaspidiformes;1;1;0;0;0;0;1;1
Anaspida;Anaspidiformes;0;0;0;0;0;0;NA;1
Anaspida;Anaspidiformes;0;1;0;0;0;0;1;1
Thelodonti;Loganelliiformes;0;0;1;0;1;0;1;1
Thelodonti;Shieliiformes;0;0;1;0;1;0;1;1
Thelodonti;Phlebolepidiformes;0;0;1;0;1;0;1;1
Thelodonti;Thelodontiformes;0;0;1;0;0;0;1;1
Thelodonti;Furcacaudiformes;0;1;0;0;1;0;0;1
Thelodonti;Furcacaudiformes;0;0;0;0;0;0;0;1
Cephalaspidimorphi;Osteostraci;0;0;1;0;2;0;0;1
Cephalaspidimorphi;Osteostraci;0;0;1;0;1;0;0;1
Cephalaspidimorphi;Osteostraci;0;0;0;0;1;0;0;1
Cephalaspidimorphi;Galeaspidiformes;0;0;0;0;0;0;0;1
Cephalaspidimorphi;Pituriaspidiformes;NA;NA;1;NA;NA;NA;NA;NA
Placodermi;Stensioellida;NA;0;1;1;1;NA;NA;1
Placodermi;Pseudopetalichthyida;NA;0;1;1;NA;NA;NA;NA
Placodermi;Rhenanida;0;0;1;1;1;0;0;1
Placodermi;Ptyctodontida;0;0;1;1;2;0;0;1
Placodermi;Petalichthyida;NA;0;1;0;0;0;0;NA
Placodermi;Phyllolepida;NA;NA;NA;1;NA;NA;NA;1
Placodermi;Arthrodira;0;0;1;1;1;0;NA;1
Placodermi;Antiarcha;0;0;1;0;1;0;0;1
Placodermi;Antiarcha;0;0;1;0;0;0;0;1
Placodermi;Antiarcha;0;0;1;1;1;0;0;NA
Chondrichthyes;Incertae_sedis;0;0;1;1;2;0;1;1

Chondrichthyes;Incertae_sedis;0;1;1;1;2;NA;1;NA

Chondrichthyes;Incertae_sedis;NA;1;1;1;NA;NA;1;1

Chondrichthyes;Polymerolepidiformes;NA;NA;NA;NA;NA;NA;1;1

Chondrichthyes;Omalodontiformes;NA;NA;1;NA;NA;NA;NA;NA

Chondrichthyes;Antarctilamniformes;NA;NA;1;NA;NA;NA;NA;NA

Chondrichthyes;Phoebodontiformes;0;0;1;1;2;0;0;1

Chondrichthyes;Phoebodontiformes;0;0;1;1;0;0;0;1

Chondrichthyes;Xenacanthiformes;0;0;1;1;1;0;1;1

Chondrichthyes;Cladoselachiformes;0;0;1;1;2;0;0;1

Chondrichthyes;Symmoriiformes;0;0;1;1;2;0;0;1

Chondrichthyes;Symmoriiformes;0;0;1;1;1;0;0;1

Chondrichthyes;Ctenacanthiformes;0;0;1;1;2;0;1;1

Chondrichthyes;Squatinactiformes;NA;NA;1;NA;NA;NA;NA;NA

Chondrichthyes;Hybodontiformes;0;0;1;1;2;0;1;1

Chondrichthyes;Synechodontiformes;NA;0;1;1;2;NA;NA;NA

Chondrichthyes;Synechodontiformes;0;0;1;1;1;0;1;1

Chondrichthyes;Hexanchiformes;0;0;1;1;1;0;1;1

Chondrichthyes;Squaliformes;0;0;1;1;2;0;0;1

Chondrichthyes;Protospinaciformes;0;0;1;1;2;0;0;1

Chondrichthyes;Pristiformes;0;0;1;1;2;0;0;1

Chondrichthyes;Pristiophoriformes;0;0;1;1;2;0;0;1

Chondrichthyes;Squatiniformes;0;0;1;1;2;0;0;1

Chondrichthyes;Heterodontiformes;0;0;1;1;2;0;1;1

Chondrichthyes;Orectolobiformes;0;0;1;1;2;0;1;1

Chondrichthyes;Lamniformes;0;0;1;1;2;0;1;1

Chondrichthyes;Carcharhiniformes;0;0;1;1;1;0;1;1

Chondrichthyes;Carcharhiniformes;0;0;1;1;2;0;1;1

Chondrichthyes;Rajiformes;0;0;1;1;0;0;0;1

Chondrichthyes;Rajiformes;0;0;1;1;2;0;0;0

Chondrichthyes;Rajiformes;0;0;1;1;2;0;0;1
Chondrichthyes;Torpediniformes;0;0;1;1;1;0;0;1
Chondrichthyes;Torpediniformes;0;0;1;1;0;0;0;1
Chondrichthyes;Torpediniformes;0;0;1;1;2;0;0;1
Chondrichthyes;Myliobatiformes;0;0;1;1;0;0;0;0
Chondrichthyes;Myliobatiformes;0;0;1;1;0;0;1;0
Chondrichthyes;Myliobatiformes;0;0;1;1;1;0;1;0
Chondrichthyes;Myliobatiformes;0;0;1;1;0;0;0;1
Chondrichthyes;Myliobatiformes;0;0;1;1;1;0;0;0
Chondrichthyes;Myliobatiformes;0;0;1;1;2;0;0;1
Chondrichthyes;Myliobatiformes;0;0;1;1;1;0;0;1
Chondrichthyes;Incertae_sedis;0;0;1;1;2;0;1;1
Chondrichthyes;Incertae_sedis;0;0;1;1;1;0;0;1
Chondrichthyes;Incertae_sedis;0;0;1;1;2;0;1;1
Chondrichthyes;Orodontiformes;0;0;1;1;1;0;0;1
Chondrichthyes;Eugeneodontiformes;0;0;1;0;1;0;0;1
Chondrichthyes;Petalodontiformes;0;0;1;1;2;0;0;1
Chondrichthyes;Iniopterygia;0;0;1;1;1;0;0;1
Chondrichthyes;Unnamed_order;0;0;1;1;1;0;1;1
Chondrichthyes;Chondrenchelyiformes;0;0;1;1;1;0;0;1
Chondrichthyes;Helodontiformes;0;0;1;1;2;0;0;1
Chondrichthyes;Menaspiformes;0;0;1;1;0;0;0;1
Chondrichthyes;Menaspiformes;0;0;1;1;2;0;1;1
Chondrichthyes;Chimaeriformes;0;0;1;1;2;0;0;1
Chondrichthyes;Chimaeriformes;0;0;1;1;2;0;1;1
Chondrichthyes;Squalorajiformes;NA;0;1;1;1;0;NA;1
Acanthodii;Incertae_sedis;0;1;1;1;2;0;1;1
Acanthodii;Incertae_sedis;0;0;1;1;2;0;1;1
Acanthodii;Climatiiformes;0;1;1;1;2;0;1;1

Acanthodii;Diplacanthiformes;0;1;1;1;2;0;1;1
Acanthodii;Diplacanthiformes;0;0;1;1;2;0;1;1
Acanthodii;Ischnacanthiformes;0;0;1;1;2;0;1;1
Acanthodii;Acanthodiformes;1;0;1;0;1;0;1;1
Acanthodii;Acanthodiformes;0;0;1;1;1;0;1;1
Acanthodii;Acanthodiformes;0;1;1;1;1;0;1;1
Actinopterygii;Incertae_sedis;0;0;1;1;2;0;1;1
Actinopterygii;Polypteriformes;0;0;1;1;1;0;1;1
Actinopterygii;Polypteriformes;0;0;1;0;1;0;1;1
Actinopterygii;Cheirolepidiformes;0;0;1;1;1;0;1;1
Actinopterygii;Aeduelliformes;0;0;1;1;1;0;1;1
Actinopterygii;Redfieldiformes;0;0;1;1;1;0;1;1
Actinopterygii;Incertae_sedis;0;0;1;1;1;0;1;1
Actinopterygii;Paleonisciformes;0;0;1;1;1;0;1;1
Actinopterygii;Paleonisciformes;0;0;1;0;1;0;1;1
Actinopterygii;Bobasatraniiformes;0;0;1;1;1;0;1;1
Actinopterygii;Tarrasiiformes;0;0;1;0;1;0;1;1
Actinopterygii;Guildayichthyiformes;0;0;1;1;1;0;1;1
Actinopterygii;Phanerorhynchiformes;0;0;1;1;1;0;1;1
Actinopterygii;Saurichthyiformes;0;0;1;1;1;0;1;1
Actinopterygii;Acipenseriformes;0;0;1;1;1;0;1;1
Actinopterygii;Incertae_sedis;0;0;1;1;1;0;1;1
Actinopterygii;Pholidopleuriformes;0;0;1;1;1;0;1;1
Actinopterygii;Perleidiformes;0;0;1;1;1;0;1;1
Actinopterygii;Peltopleuriformes;0;0;1;1;1;0;1;1
Actinopterygii;Scanilepiformes;0;0;1;1;1;0;1;1
Actinopterygii;Macrosemiiformes;0;0;1;1;1;0;1;1
Actinopterygii;Semionotiformes;0;0;1;1;1;0;1;1
Actinopterygii;Lepisosteiformes;0;0;1;1;1;0;1;1

Actinopterygii;Pycnodontiformes;0;0;1;1;1;0;1;1
Actinopterygii;Parasemionotiformes;0;0;1;1;1;0;1;1
Actinopterygii;Ionoscopiformes;0;0;1;1;2;0;1;1
Actinopterygii;Ionoscopiformes;0;0;1;1;1;0;1;1
Actinopterygii;Amiiformes;0;0;1;1;1;0;1;1
Actinopterygii;Aspidorhynchiformes;0;0;1;1;1;0;1;1
Actinopterygii;Pachycormiformes;0;0;1;1;1;0;1;1
Actinopterygii;Incertae_sedis;0;0;1;1;1;0;1;1
Actinopterygii;Pholidophoriformes;0;0;1;1;1;0;1;1
Actinopterygii;Leptolepidiformes;0;0;1;1;1;0;1;1
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Actinopterygii;Tselfatiifofmes;0;0;1;0;1;0;1;1
Actinopterygii;Ichthyodectiformes;0;0;1;1;1;0;1;1
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Actinopterygii;Elopiformes;0;0;1;1;1;0;1;1
Actinopterygii;Albuliformes;0;0;1;1;1;0;1;1
Actinopterygii;Albuliformes;0;0;1;1;1;0;1;0
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Actinopterygii;Anguilliformes;0;0;0;0;1;0;1;1
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Actinopterygii;Anguilliformes;0;0;1;0;1;0;1;0
Actinopterygii;Anguilliformes;0;0;0;0;1;0;0;0

Actinopterygii;Saccopharyngiformes;0;0;1;0;1;0;1;1
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Actinopterygii;Saccopharyngiformes;0;0;1;0;1;0;1;0
Actinopterygii;Crossognathiformes;0;0;1;1;1;0;1;1
Actinopterygii;Ellimmichthyiformes;0;0;1;1;1;0;1;1
Actinopterygii;Clupeiformes;0;0;1;1;1;0;1;1
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Actinopterygii;Clupeiformes;0;0;1;0;0;0;1;1
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Actinopterygii;Gonorynchiformes;0;0;1;1;1;0;1;1
Actinopterygii;Cypriniformes;0;0;1;1;1;0;1;1
Actinopterygii;Characiformes;0;0;1;1;1;1;1;1
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Actinopterygii;Siluriformes;0;0;0;0;1;0;1;1
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Actinopterygii;Siluriformes;0;0;1;1;0;0;1;1
Actinopterygii;Siluriformes;0;0;1;1;0;0;0;1
Actinopterygii;Siluriformes;0;0;1;0;1;0;1;1
Actinopterygii;Gymnotiformes;0;0;1;0;0;NA;1;1
Actinopterygii;Gymnotiformes;0;0;1;0;0;0;1;0
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Actinopterygii;Argentiniformes;0;0;1;1;1;0;1;1
Actinopterygii;Argentiniformes;0;0;1;0;1;0;1;1
Actinopterygii;Osmeriformes;0;0;1;1;1;0;1;1
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Actinopterygii;Salmoniformes;0;0;1;1;1;1;1;1
Actinopterygii;Esociformes;0;0;1;1;1;0;1;1
Actinopterygii;Stomiiformes;0;0;1;1;1;0;1;1
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Actinopterygii;Stomiiformes;0;0;0;0;1;0;1;1
Actinopterygii;Stomiiformes;0;0;0;1;1;0;1;1
Actinopterygii;Ateleopodiformes;0;0;1;1;1;0;1;1
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Actinopterygii;Aulopiformes;0;0;1;1;1;1;1;1
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Actinopterygii;Aulopiformes;1;0;1;1;1;1;1;1
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Actinopterygii;Lampridiformes;0;0;1;1;1;0;1;1
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Actinopterygii;Percopsiformes;0;0;1;1;1;1;1;1
Actinopterygii;Sphenocephaliformes;0;0;1;1;1;1;1;1
Actinopterygii;Gadiformes;0;0;1;1;2;0;1;1
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Actinopterygii;Mugiliformes;0;0;1;1;2;0;1;1
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Actinopterygii;Atheriniformes;1;0;1;1;2;0;1;1
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Actinopterygii;Beloniformes;0;0;1;1;1;0;1;1
Actinopterygii;Cyprinodontiformes;0;0;1;0;1;0;1;1
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Actinopterygii;Stephanoberyciformes;0;0;1;0;1;0;1;1
Actinopterygii;Stephanoberyciformes;0;0;1;1;1;0;1;1
Actinopterygii;Beryciformes;0;0;1;1;2;0;1;1
Actinopterygii;Beryciformes;0;0;1;1;1;0;1;1
Actinopterygii;Zeiformes;0;0;1;1;2;0;1;1
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Actinopterygii;Zeiformes;0;0;1;1;2;0;2;1
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Actinopterygii;Gasterosteiformes;0;0;1;1;2;0;1;1
Actinopterygii;Gasterosteiformes;0;0;1;0;2;0;1;1
Actinopterygii;Syngnathiformes;0;0;1;1;2;0;1;1
Actinopterygii;Syngnathiformes;0;0;1;1;1;0;1;1
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Actinopterygii;Syngnathiformes;0;0;0;0;1;0;0;0
Actinopterygii;Synbranchiformes;0;0;1;0;1;0;1;1
Actinopterygii;Synbranchiformes;0;0;1;0;2;0;2;1
Actinopterygii;Synbranchiformes;0;0;0;0;1;0;1;1
Actinopterygii;Scorpaeniformes;0;0;1;1;1;0;1;1
Actinopterygii;Scorpaeniformes;0;0;1;0;2;0;1;1
Actinopterygii;Scorpaeniformes;0;0;1;0;1;0;1;1
Actinopterygii;Scorpaeniformes;0;0;1;1;2;0;1;1
Actinopterygii;Perciformes;0;0;1;0;1;0;1;0
Actinopterygii;Perciformes;0;0;1;0;1;0;1;1
Actinopterygii;Perciformes;0;0;1;0;2;0;1;1
Actinopterygii;Perciformes;0;0;1;0;2;0;2;1
Actinopterygii;Perciformes;0;0;1;1;1;0;1;1
Actinopterygii;Perciformes;0;0;1;1;2;0;1;1
Actinopterygii;Perciformes;0;0;1;1;2;0;2;1
Actinopterygii;Perciformes;0;0;1;1;3;0;1;1
Actinopterygii;Pleuronectiformes;0;0;0;1;1;0;1;1
Actinopterygii;Pleuronectiformes;0;0;1;1;1;0;1;1
Actinopterygii;Tetraodontiformes;0;0;1;1;2;0;1;1
Actinopterygii;Tetraodontiformes;0;0;1;0;1;0;1;1
Actinopterygii;Tetraodontiformes;0;0;1;0;1;0;1;0

Actinopterygii;Tetraodontiformes;0;0;1;0;2;0;1;1

Sarcopterygii;Stem_sarco;0;0;1;1;2;0;1;NA

Sarcopterygii;Coelacanthiformes;0;0;1;1;2;0;1;1

Sarcopterygii;Onychodontiformes;0;0;1;1;2;0;1;1

Sarcopterygii;Porolepiformes;0;0;1;1;2;0;1;1

Sarcopterygii;Dipnoiformes;0;0;1;1;1;0;0;1

Sarcopterygii;Dipnoiformes;0;0;1;1;1;0;1;1

Sarcopterygii;Dipnoiformes;0;0;1;1;2;0;1;1

Sarcopterygii;Rhizodontiformes;0;0;1;1;2;0;1;1

Sarcopterygii;Eotetrapodiformes;NA;NA;1;1;NA;NA;1;1

Sarcopterygii;Osteolepiformes;0;0;1;1;2;0;1;1

Sarcopterygii;Elpistostegalia;0;0;1;1;0;0;0;1

Sarcopterygii;Tetrapoda;0;0;1;1;0;0;0;1

Sarcopterygii;Tetrapoda;0;0;1;1;0;0;0;0

ANNEXE E

ADDITIONAL RESULTS OF MULTIPLE CORRESPONDENCE ANALYSES

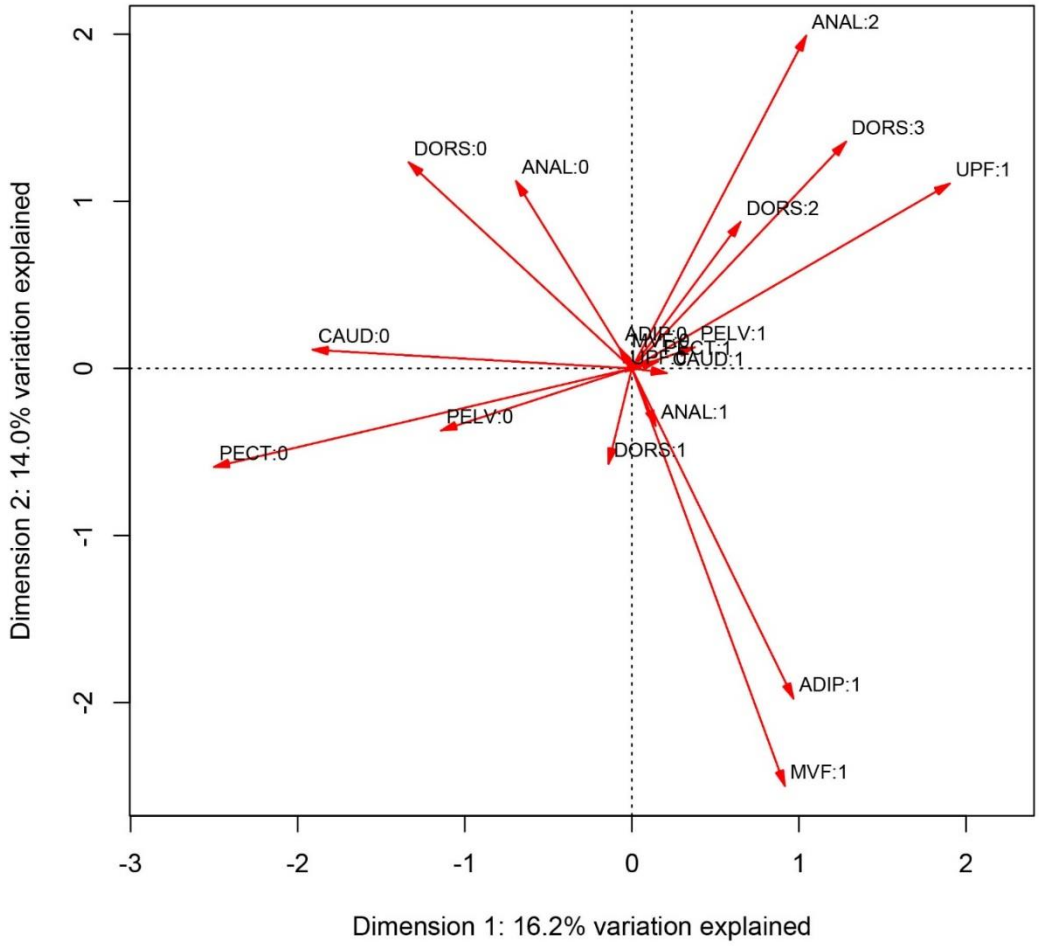

Figure E1: Biplot of the first two dimensions of the MCA focusing on gnathostomes.

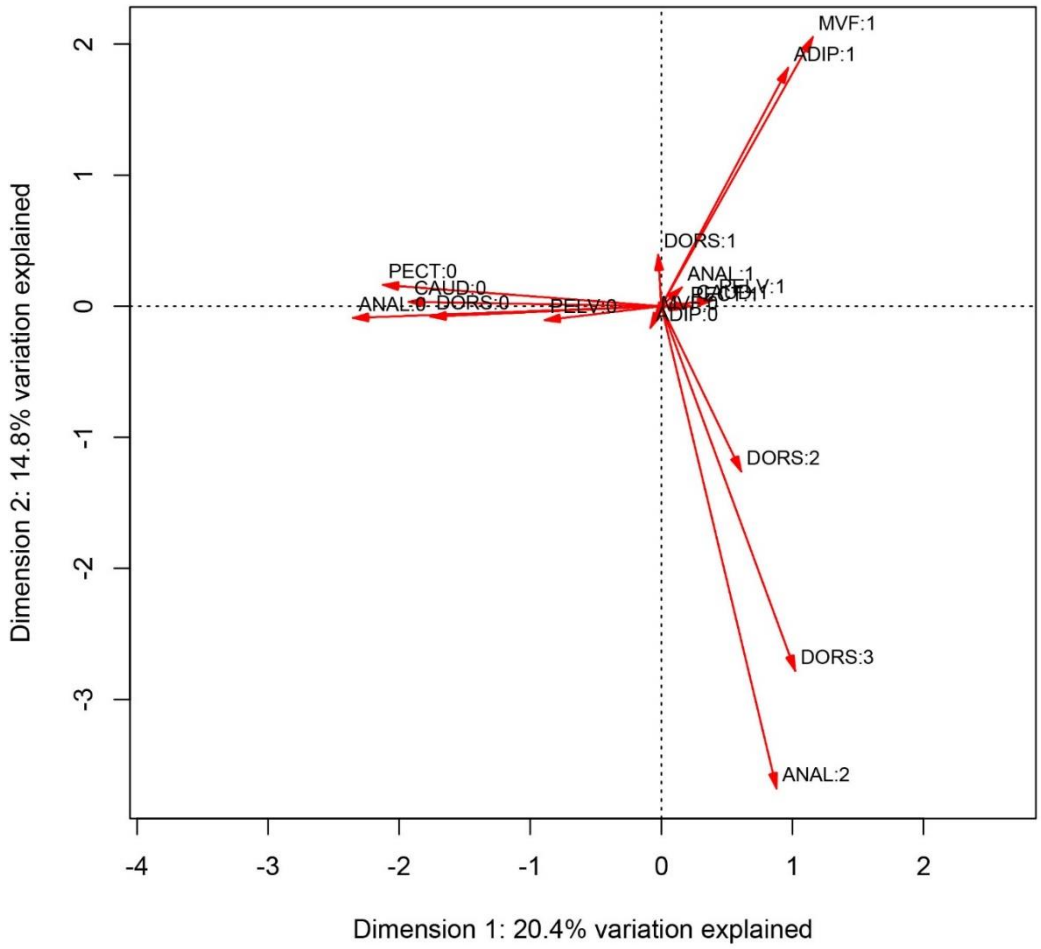

Figure E2: Biplot of the first two dimensions of the MCA focusing on osteichthyans.

Additional multiple correspondence analyses

Supplementary analyses were conducted for the total group gnathostomes and osteichthyans. These yielded results similar to those for the actinopterygian clade, differing only in the percentage of variation explained by the major axes. Multiple correspondence analyses could not be performed for placoderms alone because of a

lack of variation in fin characters. In placoderms, only two of the fins show variation: the pelvic fins, which are occasionally absent, and the dorsal fins, which can be absent, present in a single copy or duplicated.

The first two dimensions of the analysis focusing on gnathostomes explain 16.2% and 14.0% of the total variation in fin configurations, respectively. The patterns obtained for the actinopterygians are pervasive in these first two dimensions of the analysis performed on gnathostomes, although the angles between the vectors are wider. The first dimension of the MCA opposes fishes characterized by the loss of all fins to those that have either two or three dorsal and anal fins, or additional sets of fins in the form of unconstricted paired fins, median ventral fins, or adipose fins. The second dimension opposes forms having the dorsal and anal fins either absent, duplicated, or triplicated to fishes that have median ventral fins and/or adipose fins. In the analysis focusing on osteichthyans, the results are qualitatively identical as the analysis focusing on actinopterygians, although the first two dimensions of the MCA now explain 20.4% and 14.8% of the variation, respectively.

ANNEXE F

ADDITIONAL RESULTS FOR THE DANIO RERIO AND CHROSOMUS EOS DATASETS INCORPORATING ADDITIONAL MODULARITY HYPOTHESES

Table F1: Results for the zebrafish (*Danio rerio*) analyses of modularity including the novel hypotheses.

Hypothesis	Covarition ratio		Graphical modeling		Minimum deviance	
	CR	***p***	**Deviance**	**ΔAIC**	**γ***	***p***
1	0.961	0.001	61.55	1.77	-0.338	1
2	0.971	0.001	148.84	85.06	-0.101	0
3	0.957	0.005	130.98	110.98	0.021	0.003
4	0.96	0.001	220.36	166.82	-0.340	1
5	1.510	1	175.83	108.05	-0.207	0
6	0.867	0.002	154.95	85.18	-0.142	0
7	0.858	0.01	137.14	69.36	-0.037	0
8	0.893	0.002	131.46	63.68	-0.025	0
9	0.864	0.014	66.05	4.27	-0.359	1
10	1.184	0.986	185.56	111.79	-0.236	0
11	0.859	0.001	138.07	68.30	-0.025	0.001
12	0.877	0.001	184.72	110.95	-0.199	0
13	0.898	0.001	179.04	105.27	-0.186	0
14	0.902	0.001	197.35	123.57	-0.098	0
15	0.865	0.001	203.97	128.19	-0.098	0
16	0.863	0.001	185.66	109.89	-0.186	0

Hypothesis	Covarition ratio		Graphical modeling		Minimum deviance	
	CR	***p***	**Deviance**	**ΔAIC**	**γ***	***p***
17	1.149	0.986	233.64	155.86	-0.204	0
18	1.044	0.12	234.58	154.80	-0.192	0
19	1.063	0.172	266.63	184.85	-0.213	0
20	1.647	1	51.78	0	-0.141	0.96
21	1.905	1	120.57	60.80	-0.082	0.004
22	0.979	0.002	133.20	69.42	-0.151	0
23	0.956	0.001	56.28	4.51	-0.288	1
24	0.951	0.001	174.99	105.21	-0.195	0

Table F2: Results for the Northern redbelly dace (*Chrosomus eos*) analyses of modularity including the novel hypotheses.

Hypothesis	Covarition ratio		Graphical modeling		Minimum deviance	
	CR	***p***	**Deviance**	**ΔAIC**	**γ***	***p***
1	0.959	0.001	119.85	24.37	-0.271	0.862
2	0.969	0.001	202.55	103.07	-0.123	0
3	0.955	0.001	171.33	75.86	0.018	0
4	0.958	0.001	220.36	131.12	-0.272	0.885
5	1.506	1	239.60	136.12	-0.269	0
6	0.864	0.002	236.60	131.12	-0.126	0
7	0.854	0.01	205.69	102.22	0.021	0
8	0.886	0.001	177.66	74.18	0.040	0
9	0.861	0.014	143.29	45.81	-0.277	0.715
10	1.182	0.986	293.06	183.58	-0.238	0
11	0.851	0.001	220.36	114.88	0.073	0
12	0.873	0.002	277.81	168.34	-0.157	0
13	0.893	0.002	249.78	140.30	-0.136	0
14	0.896	0.001	290.48	181.01	-0.045	0
15	0.858	0.001	333.18	221.71	-0.012	0
16	0.856	0.001	292.48	181.01	-0.103	0
17	1.146	0.986	374.97	261.49	-0.177	0
18	1.038	0.106	389.64	274.16	-0.125	0
19	1.060	0.984	425.01	307.54	-0.160	0
20	1.666	1	97.17	9.70	-0.129	0.904
21	1.894	1	153.14	57.66	-0.159	0.1
22	0.978	0.002	153.48	54.00	-0.180	0

Hypothesis	Covarition ratio		Graphical modeling		Minimum deviance	
	CR	***p***	**Deviance**	**ΔAIC**	**γ***	***p***
23	0.954	0.001	87.48	0	-0.280	1
24	0.948	0.001	225.69	120.21	-0.205	0

LEXIQUE

Apomorphe : Dans le contexte d'une phylogénie, un caractère apomorphe (ou dérivé) est un caractère qui a subi une modification par rapport à la condition ancestrale. Cela s'oppose à un caractère plésiomorphe.

Atavisme : Réapparition chez un individu d'une caractéristique ancestrale qui avait disparu depuis plusieurs générations.

Endosquelette : Chez les vertébrés, le système endosquelettique est composé d'éléments osseux et cartilagineux qui servent de support et de protection du corps ou de ses parties, et qui sont sous-jacent au système tégumentaire.

Exosquelette : Chez les vertébrés, le système exosquelettique est composé d'éléments osseux et cartilagineux qui servent de support et de protection du corps ou de ses parties, et qui se développent à même l'épiderme.

Génotype : L'ensemble des gènes que possède un organisme.

Macroévolution : La macroévolution fait références à des changements phénotypiques qui se produisent à long terme et qui sont généralement d'une ampleur suffisante pour permettre d'établir des distinctions entre des espèces ou des lignées évolutives.

Microévolution : La microévolution fait références aux changements évolutifs qui se produisent à court terme au sein des populations ou des espèces.

Paedomorphose : Rétention chez l'adulte de caractères qui sont normalement associés aux phases larvaires ou juvéniles.

Paraphylie : Un groupe paraphylétique est un regroupement de taxons qui, quoiqu'ils partagent tous un même ancêtre commun, n'incluent pas la totalité des descendants de cet ancêtre commun. Cela s'oppose à un groupe monophylétique, ou clade, qui inclut l'ensemble des descendants d'un ancêtre commun.

Phénotype : Le phénotype regroupe les caractéristiques morphologiques, physiologiques, biochimiques, comportementales, ou autres, qui se manifestent au cours du cycle de vie d'un organisme et représentent l'expression de son génotype.

Plasticité phénotypique : Capacité pour un génotype donné d'exprimer plusieurs phénotypes différents en fonction de l'environnement dans lequel l'organisme se retrouve.

Pléiotropie : La pléiotropie survient lorsqu'un gène donné a des effets qui s'étendent à de multiples traits phénotypiques.

Plésiomorphe : Dans le contexte d'une phylogénie, un caractère est considéré plésiomorphe s'il correspond à l'état ancestral de ce caractère. Cela s'oppose à un caractère apomorphe.

Synapomorphie : Un caractère dérivé partagé par les membres d'un clade et qui est hérité de leur ancêtre commun.

BIBLIOGRAPHIE

Abe G, Ide H, Tamura K. 2007. Function of *FGF* signaling in the developmental process of the median fin fold in zebrafish. Developmental Biology 304(1):355-366.

Abel O. 1911. Grundzüge der Palaeobiologie der Wirbeltiere. Stuttgart, Germany: E. Schweirzerbart. 708 p.

Abel RL, Laurini CR, Richter M. 2012. A palaeobiologist's guide to 'virtual' micro-CT preparation. Palaeontologia Electronica 15(2):16.

Abou Chakra M, Hall BK, Stone JR. 2014. Using information in taxonomists' heads to resolve hagfish and lamprey relationships and recapitulate craniate-vertebrate phylogenetic history. Historical Biology 26(5):652-660.

Ackerly DD, Nyffeler R. 2004. Evolutionary diversification of continuous traits: Phylogenetic tests and application to seed size in the California flora. Evolutionary Ecology 18(3):249-272.

Ackermann RR, Cheverud JM. 2000. Phenotypic covariance structure in tamarins (genus *Saguinus*): A comparison of variation patterns using matrix correlation and common principal component analysis. American Journal of Physical Anthropology 111(4):489-501.

Adam H, Strahan R. 1963. Systematics and geographical distribution of myxinoids. In: Brodal A, Fänge R, editors. The Biology of Myxine. Oslo, Norway: Universitetsforlaget. p 1-8.

Adams DC. 2014a. A generalized K statistic for estimating phylogenetic signal from shape and other high-dimensional multivariate data. Systematic Biology 63(5):685-697.

Adams DC. 2014b. Quantifying and comparing phylogenetic evolutionary rates for shape and other high-dimensional phenotypic data. Systematic Biology 63(2):166-177.

Adams DC. 2016. Evaluating modularity in morphometric data: Challenges with the RV coefficient and a new test measure. Methods in Ecology and Evolution 7(5):565-572.

Adams DC, Otarola-Castillo E. 2013. geomorph: An R package for the collection and analysis of geometric morphometric shape data. Methods in Ecology and Evolution 4(4):393-399.

Adams DC, Rohlf FJ, Slice DE. 2013. A field comes of age: Geometric morphometrics in the 21st century. Hystrix, Italian Journal of Mammalogy 24(1):7-14.

Adrain JM, Wilson MVH. 1994. Early Devonian cephalaspids (Vertebrata, Osteostraci, Cornuata) from the Southern Mackenzie Mountains, NWT, Canada. Journal of Vertebrate Paleontology 14(3):301-319.

Adriaens D, Devaere S, Teugels GG, Dekegel B, Verraes W. 2002. Intraspecific variation in limblessness in vertebrates: A unique example of microevolution. Biological Journal of the Linnean Society 75(3):367-377.

Aguilar-Medrano R, Frédérich B, Barber PH. 2016. Modular diversification of the locomotor system in Damselfishes (Pomacentridae). Journal of Morphology 277(5):603-614.

Agulnik SI, Garvey N, Hancock S, Ruvinsky I, Chapman DL, Agulnik I, Bollag R, Papaioannou V, Silver LM. 1996. Evolution of mouse *T-box* genes by tandem duplication and cluster dispersion. Genetics 144(1):249-254.

Ahlberg PE. 1989. Paired fin skeletons and relationships of the fossil group Porolepiformes (Osteichthyes: Sarcopterygii). Zoological Journal of the Linnean Society 96(2):119-166.

Ahlberg PE. 1991. A reexamination of sarcopterygian interrelationships, with special reference to the Porolepiformes. Zoological Journal of the Linnean Society 103(3):241-287.

Ahlberg PE, Johanson Z. 1998. Osteolepiforms and the ancestry of tetrapods. Nature 395(6704):792-794.

Ahlstrom EH, Amaoka K, Hensley DA, Moser HG, Sumida BY. 1984. Pleuronectiformes: Development. In: Moser HG, Richards WJ, Cohen DM, Fahay MP, Kendall AW, Richardson SL, editors. Ontogeny and Systematics of Fishes. Based on an international symposium dedicated to the memory of Elbert Halvor Ahlstrom. Lawrence, KS: The American Society of Ichthyologists and Herpetologists. p 640-670.

Aiello BR, Stewart TA, Hale ME. 2016. Mechanosensation in an adipose fin. Proceedings of the Royal Society B-Biological Sciences 283(1826):20152794.

Akaike H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19(6):716-723.

Alberch P, Gould SJ, Oster GF, Wake DB. 1979. Size and shape in ontogeny and phylogeny. Paleobiology 5(3):296-317.

Albert JS. 2001. Species diversity and phylogenetic systematics of American knifefishes (Gymnotiformes, Teleostei). Miscellaneous Publications of the Museum of Zoology, University of Michigan(190):1-127.

Albert JS, Crampton WGR. 2009. A new species of electric knifefish, genus *Compsaraia* (Gymnotiformes: Apteronotidae) from the Amazon River, with extreme sexual dimorphism in snout and jaw length. Systematics and Biodiversity 7(1):81-92.

Albert JS, Fink WL. 2007. Phylogenetic relationships of fossil neotropical electric fishes (Osteichthyes: Gymnotiformes) from the Upper Miocene of Bolivia. Journal of Vertebrate Paleontology 27(1):17-25.

Albertson RC, Kocher TD. 2001. Assessing morphological differences in an adaptive trait: A landmark-based morphometric approach. Journal of Experimental Zoology 289(6):385-403.

Albertson RC, Kocher TD. 2006. Genetic and developmental basis of cichlid trophic diversity. Heredity 97(3):211-221.

Aldridge RJ. 1987. Conodont palaeobiology: A historical review. In: Aldridge RJ, editor. Palaobiology of Conodonts. Chichester, UK: Ellis Horwood Ltd. p 11-34.

Aldridge RJ, Briggs DEG. 1990. Sweet talk. Paleobiology 16(2):241-246.

Aldridge RJ, Briggs DEG, Clarkson ENK, Smith MP. 1986. The affinities of conodonts - New evidence from the Carboniferous of Edinburgh, Scotland. Lethaia 19:279-291.

Aldridge RJ, Briggs DEG, Smith MP, Clarkson ENK, Clark NDL. 1993. The anatomy of conodonts. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 340(1294):405-421.

Aldridge RJ, Purnell MA. 1996. The conodont controversies. Trends in Ecology & Evolution 11(11):463-468.

Aldridge RJ, Purnell MA, Gabbott SE, Theron JN. 1995. The apparatus architecture and function of *Promissum pulchrum* Kovacs-Endrody (Conodonta, Upper Ordovician) and prioniodontid plan. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 347:275-291.

Aldridge RJ, Smith MP. 1993. Conodonta. In: Benton MJ, editor. The Fossil Record 2. London, UK: Chapman & Hall. p 563-572.

Aldridge RJ, Theron JN. 1993. Conodonts with preserved soft tissue from a new Ordovician Konservat-Lagerstätte. Journal of Micropalaeontology 12:113-117.

Allen CE. 2008. The "Eyespot Module" and eyespots as modules: Development, evolution, and integration of a complex phenotype. Journal of Experimental Zoology Part B-Molecular and Developmental Evolution 310B(2):179-190.

Allen GR. 1998. A review of the marine catfish genus *Paraplotosus* (Plotosidae) with the description of a new species from north-western Australia. The Raffles Bulletin of Zoology 46(1):123-134.

Alves-Gomes JA. 1999. Systematic biology of gymnotiform and mormyriform electric fishes: Phylogenetic relationships, molecular clocks and rates of evolution in the mitochondrial rRNA genes. Journal of Experimental Biology 202(10):1167-1183.

Amesbury E, Snelson FF. 1997. Spine replacement in a freshwater population of the Atlantic stingray, *Dasyatis sabina*. Copeia 1997(1):220-223.

Andrews EA. 1893. An undescribed acraniate: *Asymmetron lucayanum*. Studies from the Biological Laboratory of Johns Hopkins University 5:213-247.

Andrews M, Long J, Ahlberg P, Barwick R, Campbell K. 2005. The structure of the sarcopterygian *Onychodus jandemarrai* n. sp. from Gogo, Western Australia: With a functional interpretation of the skeleton. Transactions of the Royal Society of Edinburgh-Earth Sciences 96:197-307.

Aristotle, Barthélémy-Saint-Hilaire J. 1883. Traités des parties des animaux et de la marche des animaux d'Aristote, Tome second. Paris: Librairie Hachette et Cie. 535 p.

Aristotle, Cresswell R, Schneider JG. 1878. Aristotle's History of Animals in Ten Books. London: George Bell & Sons. 326 p.

Arratia G. 1999. The monophyly of Teleostei and stem-group teleosts. Consensus and disagreements. In: Arratia G, Schultze H-P, editors. Mesozoic Fishes 2 – Systematics and Fossil Record. München. Germany: Verlag Dr. Friedrich Pfeil. p 265-334.

Arratia G. 2000. New teleostean fishes from the Jurassic of southern Germany and the systematic problems concerning the 'pholidophoriforms'. Paläontologische Zeitschrift 74(1/2):113-143.

Arratia G. 2008. The varasichthyid and other crossognathiform fishes, and the Break-up of Pangaea. In: Cavin L, Longbottom A, Richter M, editors. Fishes and the Break-up of Pangaea. London, UK: The Geological Society of London Special Publication Vol. 295. p 71-92.

Arratia G. 2016. New remarkable Late Jurassic teleosts from southern Germany: Ascalaboidae n. fam., its content, morphology, and phylogenetic relationships. Fossil Record 19(1):31-59.

Arratia G, Schultze H-P. 2015. A new fossil actinistian from the Early Jurassic of Chile and its bearing on the phylogeny of Actinistia. Journal of Vertebrate Paleontology 35(5):12.

Arratia G, Schultze H-P, Casciotta J. 2001. Vertebral column and associated elements in dipnoans and comparison with other fishes: Development and homology. Journal of Morphology 250(2):101-172.

Arsenault M, Desbiens S, Janvier P, Kerr J. 2004. New data on the soft tissues and external morphology of the antiarch *Bothriolepis canadensis* (Whiteaves, 1880), from the Upper Devonian of Miguasha, Quebec. In: Arratia G, Wilson MVH, Cloutier R, editors. Recent Advances in the Origin and Early Radiation of Vertebrates. München, Germany: Verlag Dr. Friedrich Pfeil. p 439-454.

Arsenault M, Janvier P. 1991. The anaspid-like craniates of the Escuminac Formation (Upper Devonian) from Miguasha (Quebec, Canada), with remarks on anaspid-petromyzontid relationships. In: Chang MM, Liu YH, Zhang GR, editors. Early Vertebrates and Related Problems of Evolutionary Biology. Beijing, China: Science Press. p 19-44.

Aschliman NC, Claeson KM, McEachran JD. 2012a. Phylogeny of Batoidea. In: Carrier JC, Musick JA, Heithaus MR, editors. Biology of Sharks and their Relatives, Second Edition. Boca Raton, FL: CRC Press. p 57-95.

Aschliman NC, Nishida M, Miya M, Inoue JG, Rosana KM, Naylor GJP. 2012b. Body plan convergence in the evolution of skates and rays (Chondrichthyes: Batoidea). Molecular Phylogenetics and Evolution 63(1):28-42.

Azariah J. 1965. On the seasonal appearance of fin rays and their bearing on the reproductive cycle of *Branchiostoma lanceolatum*. Journal of the Marine Biological Association of India 7(2):459-461.

Balfour FM. 1876. The development of elasmobranch fishes. The Journal of Anatomy and Physiology 11(1):128-172.

Balfour FM. 1878. A monograph on the development of elasmobranch fishes. London: MacMillan and Co. 295 p.

Balfour FM. 1881. On the development of the skeleton of the paired fins of Elasmobranchii, considered in relation to its bearings on the nature of the limbs of the Vertebrata. Proceedings of the Zoological Society of London 1881:656-671.

Balfour FM, Parker WN. 1882. On the structure and development of *Lepidosteus*. Philosophical Transactions of the Royal Society of London 173(7):359-442.

Ballard WW, Mellinger J, Lechenault H. 1993. A series of normal stages for development of *Scyliorhinus canicula*, the lesser spotted dogfish (Chondrichthyes, Scyliorhinidae). Journal of Experimental Zoology 267(3):318-336.

Bardack D. 1991. First fossil hagfish (Myxinoidea): A record from the Pennsylvanian of Illinois. Science 254(5032):701-703.

Bardack D. 1998. Relationships of living and fossil hagfishes. In: Jørgensen JM, Lomholt JP, Weber RE, Malte H, editors. The Biology of Hagfishes. London: Chapman & Hall. p 3-14.

Bardack D, Richardson ES. 1977. New agnathous fishes from the Pennsylvanian of Illinois. Fieldiana, Geology 33(26):489-512.

Bardack D, Zangerl R. 1968. First fossil lamprey: A record from the Pennsylvanian of Illinois. Science 162(3859):1265-1267.

Baum BR. 1992. Combining trees as a way of combining data sets for phylogenetic inference, and the desirability of combining gene trees. Taxon 41(1):3-10.

Baum BR, Ragan MA. 2004. The MRP method. In: Bininda-Emonds ORP, editor. Phylogenetic Supertrees - Combining Information to Reveal the Tree of Life. Dordrecht, Netherlands: Kluwer Academic Publishers. p 17-34.

Bean BA, Weed AC. 1909a. Description of a new skate (*Dactylobatus armatus*) from deep water off the southern Atlantic coast of the United States. Proceedings of the United States National Museum 36:459-461.

Bean BA, Weed AC. 1909b. Descriptions of two new species of electric rays, of the family Narcobatidae, from deep water off the southern Atlantic coast of the Unitd States. Proceedings of the United States National Museum 36:677-680.

Béchard I, Arsenault F, Cloutier R, Kerr J. 2014. The Devonian placoderm fish *Bothriolepis canadensis* revisited with three-dimensional digital imagery. Palaeontologia Electronica 17(1):19.

Belon P. 1551. L'histoire naturelle des estranges poissons marins. Paris: Imprimerie de Regnaud Chaudiere. 55 p.

Bemis WE. 1984. Paedomorphosis and the evolution of the Dipnoi. Paleobiology 10(3):293-307.

Bemis WE, Grande L. 1999. Development of the median fins of the North American paddlefish (*Polyodon spathula*), and a reevaluation of the lateral fin-fold hypothesis. In: Arratia G, Schultze H-P, editors. Mesozoic Fishes 2 – Systematics and Fossil Record. München: Verlag Dr. Friedrich Pfeil. p 41-68.

Bergström J, Naumann WW, Viehweg J, Martí- Mus M. 1998. Conodonts, calcichordates and the origin of vertebrates. Fossil Record 1(1):81-91.

Berrill NJ. 1930. Studies in tunicate development. Part I. General physiology of development of simple ascidians. Philosophical Transactions of the Royal Society of London. Series B 218:37-78.

Betancur-R R, Broughton RE, Wiley EO, Carpenter K, López JA, Li C, Holcroft NI, Arcila D, Sanciangco M, Cureton JC and others. 2013. The tree of life and a new classification of bony fishes. PLoS Currents Tree of Life:1-41.

Beznosov P. 2009. A redescription of the Early Carboniferous acanthodian *Acanthodes lopatini* Rohon, 1889. Acta Zoologica 90(Suppl. 1):183-193.

Bigelow HB, Farfante IP. 1948. Lancelets. In: Tee-Van J, Breder CM, Hildebrand SF, Parr AE, Schroeder WC, editors. Fishes of the Western North Atlantic. Part 1. Lancelets, Cyclostomes, Sharks. New Haven: Sears Foundation for Marine Research, Yale University. p 1-28.

Bigelow HB, Schroeder WC. 1953. Sawfishes, guitarfishes, skates and rays. In: Tee-Van J, Breder CM, Parr AE, Schroeder WC, Schultz LP, editors. Fishes of the Western North Atlantic. Part 2. Sawfishes, Guitarfishes, Skates and Rays, Chimaeroids. New Haven: Sears Foundation for Marine Research, Yale University. p 1-514.

Bigelow HB, Schroeder WC. 1958. Four new rajids from the Gulf of Mexico. Bulletin of the Museum of Comparative Zoology 119(2):201-233.

Bininda-Emonds ORP. 2004. New uses for old phylogenies - An introduction to the volume. In: Bininda-Emonds ORP, editor. Phylogenetic Supertrees - Combining Information to Reveal the Tree of Life. Dordrecht, Netherlands: Kluwer Academic Publishers. p 1-14.

Bininda-Emonds ORP, Bryant HN. 1998. Properties of matrix representation with parsimony analyses. Systematic Biology 47(3):497-508.

Bininda-Emonds ORP, Gittleman JL, Purvis A. 1999. Building large trees by combining phylogenetic information: A complete phylogeny of the extant Carnivora (Mammalia). Biological Reviews 74(2):143-175.

Bininda-Emonds ORP, Gittleman JL, Steel MA. 2002. The (Super)tree of life: Procedures, problems, and prospects. Annual Review of Ecology and Systematics 33:265-289.

Bininda-Emonds ORP, Jones KE, Price SA, Cardillo M, Grenyer R, Purvis A. 2004. Garbage in, garbage out: Data issues in supertree construction. In: Bininda-Emonds ORP, editor. Phylogenetic Supertrees - Combining Information to Reveal the Tree of Life. Dordrecht, Netherlands: Kluwer Academic Publishers. p 267-280.

Bininda-Emonds ORP, Sanderson MJ. 2001. Assessment of the accuracy of matrix representation with parsimony analysis supertree construction. Systematic Biology 50(4):565-579.

Blair JE, Hedges SB. 2005. Molecular phylogeny and divergence times of deuterostome animals. Molecular Biology and Evolution 22(11):2275-2284.

Blieck A. 1984. Les hétérostracés ptéraspidiformes, agnathes du Silurien-Dévonien du continent Nord-Atlantique et des blocs avoisinants: Révision systématique,

phylogénie, biostratigraphie, biogéographie. Paris, France: Centre National de la Recherche Scientifique. 199 p.
Blieck A. 2011. From adaptive radiations to biotic crises in Palaeozoic vertebrates: A geobiological approach. Geologica Belgica 14(3-4):203-227.
Blieck A, Janvier P. 1991. Silurian vertebrates. Special Papers in Palaeontology(44):345-389.
Blieck A, Turner S, Burrow CJ, Schultze H-P, Rexroad CB, Bultynck P, Nowlan GS. 2010. Fossils, histology, and phylogeny: Why conodonts are not vertebrates. Episodes 33(4):234-241.
Blom H. 2008. A new anaspid fish from the Middle Silurian Cowie Harbour fish bed of Stonehaven, Scotland. Journal of Vertebrate Paleontology 28(3):594-600.
Blom H. 2012. New birkeniid anaspid from the Lower Devonian of Scotland and its phylogenetic implications. Palaeontology 55:641-652.
Blom H, Märss T. 2010. The interrelationships and evolutionary history of anaspids. In: Elliott DK, Maisey JG, Yu X, Miao D, editors. Morphology, Phylogeny and Paleobiogeography of Fossil Fishes. München, Germany: Verlag Dr. Friedrich Pfeil. p 45-58.
Blom H, Märss T, Miller CG. 2002. Silurian and earliest Devonian birkeniid anaspids from the Northern Hemisphere. Transactions of the Royal Society of Edinburgh-Earth Sciences 92:263-323.
Blomberg SP, Garland T, Ives AR. 2003. Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. Evolution 57(4):717-745.
Boisvert CA. 2005. The pelvic fin and girdle of *Panderichthys* and the origin of tetrapod locomotion. Nature 438(7071):1145-1147.
Boisvert CA, Mark-Kurik E, Ahlberg PE. 2008. The pectoral fin of *Panderichthys* and the origin of digits. Nature 456(7222):636-638.
Bolin RL. 1939. A new stomiatoid fish from California. Copeia 1939(1):39-41.
Bolker JA. 2000. Modularity in development and why it matters to evo-devo. American Zoologist 40(5):770-776.
Bolker JA. 2005. Defining a meeting place: Modularity in development and evolution. Evolution 59(6):1383-1386.
Bonner JT. 1988. The evolution of complexity by means of natural selection. Princeton, NJ: Princeton University Press. 260 p.
Bookstein FL. 1991. Morphometric tools for landmark data: Geometry and biology. New York: Cambridge University Press. 435 p.
Bookstein FL. 1997. Landmark methods for forms without landmarks: Morphometrics of group differences in outline shape. Medical Image Analysis 1(3):225-243.
Boulenger GA. 1898. On a collection of fishes from the Rio Jurua, Brazil. Transactions of the Zoological Society of London 14(7):421-427.
Bourlat SJ, Juliusdottir T, Lowe CJ, Freeman R, Aronowicz J, Kirschner M, Lander ES, Thorndyke M, Nakano H, Kohn AB and others. 2006. Deuterostome phylogeny reveals monophyletic chordates and the new phylum Xenoturbellida. Nature 444(7115):85-88.

Brandon RN. 1999. The units of selection revisited: The modules of selection. Biology & Philosophy 14(2):167-180.

Brazeau MD. 2009. The braincase and jaws of a Devonian 'acanthodian' and modern gnathostome origins. Nature 457(7227):305-308.

Brazeau MD. 2012. A revision of the anatomy of the Early Devonian jawed vertebrate *Ptomacanthus anglicus* Miles. Palaeontology 55:355-367.

Brazeau MD, de Winter V. 2015. The hyoid arch and braincase anatomy of *Acanthodes* support chondrichthyan affinity of 'acanthodians'. Proceedings of the Royal Society B-Biological Sciences 282(1821):6.

Brazeau MD, Friedman M. 2015. The origin and early phylogenetic history of jawed vertebrates. Nature 520(7548):490-497.

Bridge TW. 1904. Fishes (Exclusive of the systematic account of Teleostei). In: Harmer SF, Shipley AE, editors. The Cambridge Natural History. Volume VII. London, UK: McMillan and Co. Limited. p 141-537.

Briggs DEG. 1992. A major extinct group added to the vertebrates. Science 256(5061):1285-1286.

Briggs DEG, Clarkson ENK, Aldridge RJ. 1983. The conodont animal. Lethaia 16:1-14.

Briggs DEG, Kear AJ. 1994. Decay of *Branchiostoma* - Implications for soft-tissue preservation in conodonts and other primitive chordates. Lethaia 26(4):275-287.

Brito PM. 2000. A new halecomorph with two dorsal fins, *Placidichthys bidorsalis* n. g., n. sp. (Actinopterygii : Halecomorphi) from the Lower Cretaceous of the Araripe Basin, northeast Brazil. Comptes Rendus de l'Académie des Sciences Série II Fascicule a - Sciences de la Terre et des Planètes 331(11):749-754.

Brito PM, Alvarado-Ortega J. 2008. A new species of *Placidichthys* (Halecomorphi: Ionoscopiformes) from the Lower Cretaceous Marizal Formation, northeastern Brazil, with a review of the biogeographical distribution of the Ophiopsidae. Geological Society, London, Special Publications 295:145-154.

Britz R, Conway KW. 2009. Osteology of *Paedocypris*, a miniature and highly developmentally truncated fish (Teleostei: Ostariophysi: Cyprinidae). Journal of Morphology 270(4):389-412.

Britz R, Johnson GD. 2012. Ontogeny and homology of the skeletal elements that form the sucking disc of remoras (Teleostei, Echeneoidei, Echeneidae). Journal of Morphology 273(12):1353-1366.

Broughton RE, Betancur-R R, Li C, Arratia G, Ortí G. 2013. Multilocus phylogenetic analysis reveals the
pattern and tempo of bony fish evolution. PLoS Currents Tree of Life:1-33.

Brusatte SL, Montanari S, Yi HY, Norell MA. 2011. Phylogenetic corrections for morphological disparity analysis: New methodology and case studies. Paleobiology 37(1):1-22.

Bryant HN. 2004. The cladistics of matrix representation with parsimony. In: Bininda-Emonds ORP, editor. Phylogenetic Supertrees - Combining Information to

Reveal the Tree of Life. Dordrecht, Netherlands: Kluwer Academic Publishers. p 353-368.

Buckland-Nicks JA, Gillis M, Reimchen TE. 2012. Neural network detected in a presumed vestigial trait: ultrastructure of the salmonid adipose fin. Proceedings of the Royal Society B-Biological Sciences 279(1728):553-563.

Budney LA, Hall BK. 2010. Comparative morphology and osteology of pelvic fin-derived midline suckers in lumpfishes, snailfishes and gobies. Journal of Applied Ichthyology 26(2):167-175.

Burrow C, den Blaauwen J, Newman M, Davidson R. 2016. The diplacanthid fishes (Acanthodii, Diplacanthiformes, Diplacanthidae) from the Middle Devonian of Scotland. Palaeontologia Electronica 19.1.10A:1-83.

Burrow CJ. 2004. Acanthodian fishes with dentigerous jaw bones: The Ischnacanthiformes and *Acanthodopsis*. Fossils and Strata(50):8-22.

Burrow CJ. 2007. Early Devonian (Emsian) acanthodian faunas of the western USA. Journal of Paleontology 81(5):824-840.

Burrow CJ, Newman MJ, Davidson RG, den Blaauwen JL. 2013. Redescription of *Parexus recurvus*, an Early Devonian acanthodian from the Midland Valley of Scotland. Alcheringa 37(3):392-414.

Burrow CJ, Rudkin D. 2014. Oldest near-complete acanthodian: The first vertebrate from the Silurian Bertie Formation Konservat-Lagerstatte, Ontario. PLoS One 9(8):e104171.

Burrow CJ, Turner S. 2010. Reassessment of "*Protodus*" *scoticus* from the Early Devonian of Scotland. In: Elliott DK, Maisey JG, Yu X, Miao D, editors. Morphology, Phylogeny and Paleobiogeography of Fossil Fishes. München, Germany: Verlag Dr. Friedrich Pfeil. p 123-144.

Burrow CJ, Young GC. 2005. The acanthodian fauna of the Craven Peaks Beds (Early to Middle Devonian), Western Queensland. Memoirs of the Queensland Museum 51(1):3-25.

Burrow CJ, Young GC. 2012. New information on *Culmacanthus* (Acanthodii: Diplacanthiformes) from the ?Early–Middle Devonian of Southeastern Australia. Proceedings of the Linnean Society of New South Wales 134:21-29.

Butler MA, King AA. 2004. Phylogenetic comparative analysis: A modeling approach for adaptive evolution. American Naturalist 164(6):683-695.

Capdevila J, Izpesúa Belmonte JC. 2001. Patterning mechanisms controlling vertebrate limb development. Annual Review of Cell and Developmental Biology 17:87-132.

Carr RK. 1995. Placoderm diversity and evolution. Bulletin du Muséun national d'Histoire naturelle. 4^{ieme} Série. Section C, Sciences de la Terre, Paléontologie, Géologie, Minéralogie 17(1-4):85-125.

Carr RK, Johanson Z, Ritchie A. 2009. The phyllolepid placoderm *Cowralepis mclachlani*: Insights into the evolution of feeding mechanisms in jawed vertebrates. Journal of Morphology 270(7):775-804.

Cavin L. 2010. Diversity of Mesozoic semionotiform fishes and the origin of gars (Lepisosteidae). Naturwissenschaften 97(12):1035-1040.

Cavin L, Suteethorn V. 2006. A new semionotiform (Actinopterygii, Neopterygii) from Upper Jurassic - Lower Cretaceous deposits of north-east Thailand, with comments on the relationships of semionotiforms. Palaeontology 49:339-353.

Chang M-M, Yu X. 1997. Reexamination of the relationship of Middle Devonian osteolepids - Fossil characters and their interpretations. American Museum Novitates 3189:1-20.

Chang MM, Wu FX, Miao DS, Zhang JY. 2014. Discovery of fossil lamprey larva from the Lower Cretaceous reveals its three-phased life cycle. Proceedings of the National Academy of Sciences of the United States of America 111(43):15486-15490.

Chang MM, Zhang JY, Miao DD. 2006. A lamprey from the Cretaceous Jehol biota of China. Nature 441(7096):972-974.

Charest F, Cloutier R. 2008. Evolution of median fins modularity in osteichthyans. Journal of Vertebrate Paleontology 28(3):63A.

Chen AL, Huang DY. 2006. Gill rays found on the early Cambrian primitive vertebrate *Yunnanozoon*. Acta Palaeontologica Sinica 45(3):345-350.

Chen AL, Huang DY. 2008. Gill rays of primitive vertebrate *Yunnanozoon* from Early Cambrian: A first record. Frontiers of Biology in China 3(2):241-244.

Chen J-Y, Dzik J, Edgecombe GD, Ramsköld L, Zhou G-Q. 1995. A possible Early Cambrian chordate. Nature 377(6551):720-722.

Chen JY, Huang DY, Li CW. 1999. An early Cambrian craniate-like chordate. Nature 402(6761):518-522.

Chen JY, Huang DY, Peng QQ, Chi HM, Wang XQ, Feng M. 2003. The first tunicate from the Early Cambrian of South China. Proceedings of the National Academy of Sciences of the United States of America 100(14):8314-8318.

Chen JY, Li CW. 1997. Early Cambrian chordate from Chengjiang, China. Bulletin of National Museum of Natural Sciences Taiwan 10:257-273.

Chernoff B, Magwene PM. 1999. Afterword - Morphological integration: Forty years later. Olson, E.C., Miller, C. G. Morphological integration. Chicago, IL: The University of Chicago Press. p 319-353.

Cheverud JM. 1982. Phenotypic, genetic, and environmental morphological integration in the cranium. Evolution 36(3):499-516.

Cheverud JM. 1996a. Developmental integration and the evolution of pleiotropy. American Zoologist 36(1):44-50.

Cheverud JM. 1996b. Quantitative genetic analysis of cranial morphology in the cotton-top (*Saguinus oedipus*) and saddle back (*S. fuscicollis*) tamarins. Journal of Evolutionary Biology 9(1):5-42.

Cheverud JM, Hartman SE, Richtsmeier JT, Atchley WR. 1991. A quantitative genetic analysis of localized morphology in mandibles of inbred mice using finite element scaling analysis. Journal of Craniofacial Genetics and Developmental Biology 1991(11):122-137.

Cheverud JM, Wagner GP, Dow MM. 1989. Methods for the comparative analysis of variation patterns. Systematic Zoology 38(3):201-213.

Chown SL, Sorensen JG, Sinclair BJ. 2008. Physiological variation and phenotypic plasticity: A response to 'Plasticity in arthropod cryotypes' by Hawes and Bale. Journal of Experimental Biology 211(21):3353-3357.

Claverie T, Patek SN. 2013. Modularity and rates of evolutionary change in a power-amplified prey capture system. Evolution 67(11):3191-3207.

Clements T, Dolocan A, Martin P, Purnell MA, Vinther J, Gabbott SE. 2016. The eyes of *Tullimonstrum* reveal a vertebrate affinity. Nature 532(7600):500-503.

Cloney RA. 1982. Ascidian larvae and the events of metamorphosis. American Zoologist 22(4):817-826.

Cloutier R. 1991. Patterns, trends, and rates of evolution within the Actinistia. Environmental Biology of Fishes 32(1-4):23-58.

Cloutier R. 2010. The fossil record of fish ontogenies: Insights into developmental patterns and processes. Seminars in Cell & Developmental Biology 21(4):400-413.

Cloutier R, Ahlberg PE. 1995. Sarcopterygian interrelationships: How far are we from a phylogenetic consensus? Geobios M.S.(19):241-248.

Cloutier R, Ahlberg PE. 1996. Morphology, characters, and the interrelationships of basal sarcopterygians. In: Stiassny MLJ, Parenti LR, Johnson GD, editors. Interrelationships of Fishes. San Diego, CA: Academic Press. p 445-479.

Cloutier R, Arratia G. 2004. Early diversification of actinopterygians. In: Arratia G, Wilson MVH, Cloutier R, editors. Recent Advances in the Origin and Early Radiation of Vertebrates. München, Germany: Verlag Dr. Friedrich Pfeil. p 217-270.

Cloutier R, Caron A, Grünbaum T, Le Francois NR. 2010. Effect of water velocity on the timing of skeletogenesis in the Arctic charr, *Salvelinus alpinus* (Salmoniformes: Teleostei): An empirical case of developmental plasticity. International Journal of Zoology 2010(Article ID 470546):1-15.

Cloutier R, Schultze H-P. 1996. Porolepiform fishes (Sarcopterygii). In: Schultze H-P, Cloutier R, editors. Devonian Fishes and Plants of Miguasha, Quebec, Canada. München, Germany: Verlag Dr. Friedrich Pfeil. p 248-270.

Coates MI. 1993. *Hox* genes, fin folds and symmetry. Nature 364(6434):195-196.

Coates MI. 1994. The origin of vertebrate limbs. Development 1994 Supplement:169-180.

Coates MI. 1999. Endocranial preservation of a Carboniferous actinopterygian from Lancashire, UK, and the interrelationships of primitive actinopterygians. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 354(1382):435-462.

Coates MI. 2003. The evolution of paired fins. Theory in Biosciences 122(2-3):266-287.

Coates MI, Cohn MJ. 1998. Fins, limbs, and tails: Outgrowths and axial patterning in vertebrate evolution. Bioessays 20(5):371-381.

Coates MI, Cohn MJ. 1999. Vertebrate axial and appendicular patterning: The early development of paired appendages. American Zoologist 39(3):676-685.

Coates MI, Jeffery JE, Ruta M. 2002. Fins to limbs: What the fossils say. Evolution & Development 4(5):390-401.

Coates MI, Sequeira SEK. 2001a. Early sharks and primitive gnathostome interrelationships. In: Ahlberg PE, editor. Major Events in Early Vertebrate Evolution: Palaeontology, Phylogeny, Genetics and Development. London: Taylor & Francis. p 241-262.

Coates MI, Sequeira SEK. 2001b. A new stethacanthid chondrichthyan from the Lower Carboniferous of Bearsden, Scotland. Journal of Vertebrate Paleontology 21(3):438-459.

Cohn MJ, Izpisúa-Belmonte JC, Abud H, Heath JK, Tickle C. 1995. Fibroblast Growth Factors induce additional limb developement from the flank of chick embryos. Cell 80(5):739-746.

Collar DC, Near TJ, Wainwright PC. 2005. Comparative analysis of morphological diversity: Does disparity accumulate at the same rate in two lineages of centrarchid fishes? Evolution 59(8):1783-1794.

Collar DC, Wainwright PC, Alfaro ME, Revell LJ, Mehta RS. 2014. Biting disrupts integration to spur skull evolution in eels. Nature Communications 5(5505):1-9.

Compagno LJV. 1973. Interrelationships of living elasmobranchs. Zoological Journal of the Linnean Society 53(Suppl. 1):15-61.

Compagno LJV. 1977. Relationships of living sharks and rays. American Zoologist 17(2):303-322.

Compagno LJV, Dando M, Fowler S. 2005. Sharks of the World. Princeton, NJ: Princeton University Press. 368 p.

Cormack AM. 1963. Representation of a function by its line integrals, with some radiological applications. Journal of Applied Physics 34(9):2722-2727.

Crotwell PL, Clark TG, Mabee PM. 2001. *Gdf5* is expressed in the developing skeleton of median fins of late-stage zebrafish, *Danio rerio*. Development Genes and Evolution 211(11):555-558.

Crotwell PL, Mabee PM. 2007. Gene expression patterns underlying proximal-distal skeletal segmentation in late-stage zebrafish, *Danio rerio*. Developmental Dynamics 236(11):3111-3128.

Crotwell PL, Sommervold AR, Mabee PM. 2004. Expression of *bmp2a* and *bmp2b* in late-stage zebrafish median fin development. Gene Expression Patterns 5(2):291-296.

Cuvier G. 1849. The animal kingdom, arranged after its organization, forming a natural history of animals and an introduction to comparative anatomy, Second edition. London: WM. S. Orr and Co. 718 p.

Cuvier G, Duméril M. 1835. Leçons d'anatomie comparée de Georges Cuvier. Paris: Crochard et Cie. 587 p.

Cuvier G, Valenciennes M. 1828. Histoire naturelle des poissons, Tome premier. Paris: F.G. Levrault. 573 p.

Daeschler EB, Shubin NH, Jenkins FA. 2006. A Devonian tetrapod-like fish and the evolution of the tetrapod body plan. Nature 440(7085):757-763.

Davesne D, Friedman M, Barriel V, Lecointre G, Janvier P, Gallut C, Otero O. 2014. Early fossils illuminate character evolution and interrelationships of Lampridiformes (Teleostei, Acanthomorpha). Zoological Journal of the Linnean Society 172(2):475-498.

Davis PD, Finarelli JA, Coates MI. 2012. *Acanthodes* and shark-like conditions in the last common ancestor of modern gnathostomes. Nature 486:247-251.

Day JJ, Cotton JA, Barraclough TG. 2008. Tempo and mode of diversification of Lake Tanganyika cichlid fishes. PLoS One 3(3):10.

de Carvalho MR. 1996. Higher-level elasmobranch phylogeny, basal squaleans, and paraphyly. In: Stiassny MLJ, Parenti LR, Johnson GD, editors. Interrelationships of Fishes. San Diego, CA: Academic Press. p 35-62.

de Carvalho MR, Maisey JG. 1996. Phylogenetic relationships of the Late Jurassic shark *Protospinax* Woodward 1919 (Chondrichthyes: Elasmobranchii). In: Arratia G, Viohl G, editors. Mesozoïc Fishes - Systematics and Paleoecology. München, Germany: Verlag Dr. Friedrich Pfeil. p 9-46.

de Santana CD, Vari RP, Wosiacki WB. 2013. The untold story of the caudal skeleton in the electric eel (Ostariophysi: Gymnotiformes: *Electrophorus*). PLoS One 8(7):8.

Dean B. 1907. Notes on acanthodian sharks. American Journal of Anatomy 7(2):209-222.

Delarbre C, Gallut C, Barriel V, Janvier P, Gachelin G. 2002. Complete mitochondrial DNA of the hagfish, *Eptatretus burgeri*: The comparative analysis of mitochondrial DNA sequences strongly supports the cyclostome monophyly. Molecular Phylogenetics and Evolution 22(2):184-192.

Delbarre DJ, Davesne D, Friedman M. 2015. Anatomy and relationships of *Aipichthys pretiosus* and '*Aipichthys*' *nuchalis* (Acanthomorpha: Lampridomorpha), with a review of Late Cretaceous relatives of oarfishes and their allies. Journal of Systematic Palaeontology 14(7):545-567.

Delsuc F, Brinkmann H, Chourrout D, Philippe H. 2006. Tunicates and not cephalochordates are the closest living relatives of vertebrates. Nature 439(7079):965-968.

Delsuc F, Tsagkogeorga G, Lartillot N, Philippe H. 2008. Additional molecular support for the new chordate phylogeny. Genesis 46(11):592-604.

Denison RH. 1951. Evolution and classification of the Osteostraci. Fieldiana, Geology 11(3):157-196.

Denison RH. 1978. Volume 2 - Placodermi. Schultze H-P, editor. Stuttgart, New York: Gustav Fischer Verlag. 128 p.

Denison RH. 1979. Volume 5 - Acanthodii. Schultze H-P, editor. Stuttgart, New York: Gustav Fischer Verlag. 62 p.

Denton JSS, Adams DC. 2015. A new phylogenetic test for comparing multiple high-dimensional evolutionary rates suggests interplay of evolutionary rates and modularity in lanternfishes (Myctophiformes; Myctophidae). Evolution 69(9):2425-2440.

DeWitt TJ, Scheiner SM. 2004. Phenotypic variation from single genotypes: A primer. In: DeWitt TJ, Scheiner SM, editors. Phenotypic Plasticity: Functional and Conceptual Approaches. Oxford, UK: Oxford University Press. p 1-9.

Didier DA. 1995. Phylogenetic systematics of extant chimaeroid fishes (Holocephali, Chimaeroidei). American Museum Novitates(3119):1-86.

Didier DA, Kemper JM, Ebert DA. 2012. Phylogeny, biology, and classification of extant holocephalans. In: Carrier JC, Musick JA, Heithaus MR, editors. Biology of Sharks and their Relatives, Second Edition. Boca Raton, FL: CRC Press. p 97-122.

Didier DA, Leclair EE, Vanbuskirk DR. 1998. Embryonic staging and external features of development of the chimaeroid fish, *Callorhinchus milli* (Holocephali, Callorhinchidae). Journal of Morphology 236(1):25-47.

Dineley DL. 1994. Cephalaspids from the Lower Devonian of Prince of Wales Island, Canada. Palaeontology 37(1):61-70.

Dineley DL, Loeffler EJ. 1976. Ostracoderm faunas from the Delorme and associated Siluro-Devonian formations, North West Territories, Canada. Special Papers in Palaeontology(18):1-214.

Dingerkus G. 1979. Chordate cytogenetic studies: An analysis of their phylogenetic implications with particular reference to fishes and the living coelacanth. Occasional Papers of the California Academy of Sciences(134):111-127.

Dollo L. 1895. Sur la phylogénie des dipneustes. Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie. Bruxelles 9:79-128.

Donoghue PCJ, Forey PL, Aldridge RJ. 2000. Conodont affinity and chordate phylogeny. Biological Reviews 75(2):191-251.

Donoghue PCJ, Purnell MA, Aldridge RJ. 1998. Conodont anatomy, chordate phylogeny and vertebrate classification. Lethaia 31(3):211-219.

Donoghue PCJ, Smith MP. 2001. The anatomy of *Turinia pagei* (Powrie), and the phylogenetic status of the Thelodonti. Transactions of the Royal Society of Edinburgh-Earth Sciences 92:15-37.

Donovan LA, Mason CM, Bowsher AW, Goolsby EW, Ishibashi CDA. 2014. Ecological and evolutionary lability of plant traits affecting carbon and nutrient cycling. Journal of Ecology 102(2):302-314.

Dornburg A, Townsend JP, Friedman M, Near TJ. 2014. Phylogenetic informativeness reconciles ray-finned fish molecular divergence times. BMC Evolutionary Biology 14:14.

Dosay-Akbulut M. 2006. Specification of phylogenetic interrelations between skate-rays and sharks. Journal of Evolutionary Biochemistry and Physiology 42(2):128-133.

Douady CJ, Dosay M, Shivji MS, Stanhope MJ. 2003. Molecular phylogenetic evidence refuting the hypothesis of Batoidea (rays and skates) as derived sharks. Molecular Phylogenetics and Evolution 26(2):215-221.

Draghi J, Wagner GR. 2008. Evolution of evolvability in a developmental model. Evolution 62(2):301-315.

Drucker EG, Lauder GV. 2001. Locomotor function of the dorsal fin in teleost fishes: Experimental analysis of wake forces in sunfish. Journal of Experimental Biology 204(17):2943-2958.

Drucker EG, Lauder GV. 2002. Wake dynamics and locomotor function in fishes: Interpreting evolutionary patterns in pectoral fin design. Integrative and Comparative Biology 42(5):997-1008.

Duméril AMC. 1806. Zoologie Analytique, ou Méthode Naturelle de Classification des Animaux. Paris, France: Imprimerie de H. L. Perronneau. 344 p.

Dunn CW, Hejnol A, Matus DQ, Pang K, Browne WE, Smith SA, Seaver E, Rouse GW, Obst M, Edgecombe GD and others. 2008. Broad phylogenomic sampling improves resolution of the animal tree of life. Nature 452(7188):745-U5.

Dunn KA, Morrissey JF. 1995. Molecular phylogeny of elasmobranchs. Copeia 1995(3):526-531.

Dupret V, Sanchez S, Goujet D, Tafforeau P, Ahlberg PE. 2014. A primitive placoderm sheds light on the origin of the jawed vertebrate face. Nature 507(7493):500-503.

Dzik J. 1991. Evolution of oral apparatuses in the conodont chordates. Acta Palaeontologica Polonica 36(3):265-323.

Dzik J. 1995. *Yunnanozoon* and the ancestry of chordates. Acta Palaeontologica Polonica 40(4):341-360.

Eble GJ. 2005. Morphological modularity and macroevolution: Conceptual and empirical aspects. In: Callebaut W, Rasskin-Gutman D, editors. Modularity: Understanding the Development and Evolution of Natural Complex Systems. Cambridge, MA: MIT Press. p 221-238.

Edwards D. 1995. Introduction to graphical modelling. New York, NY: Springer-Verlag. 274 p.

Edwards D. 2000. Introduction to graphical modelling. Second edition. New York, NY: Springer-Verlag. 352 p.

Edwards D. 2004. MIM - A program for graphical modelling. Version 3.2.0.7.

Ehehalt F, Wang BG, Christ B, Patel K, Huang RJ. 2004. Intrinsic cartilage-forming potential of dermomyotomal cells requires ectodermal signals for the development of the scapula blade. Anatomy and Embryology 208(6):431-437.

Elliott DK. 1987. A reassessment of *Astraspis desiderata*, the oldest North American vertebrate. Science 237(4811):190-192.

Engeszer RE, Patterson LB, Rao AA, Parichy DM. 2007. Zebrafish in the wild: A review of natural history and new notes from the field. Zebrafish 4(1):21-40.

Eschmeyer WN, Fricke R, Fong JD, Polack DA. 2010. Marine fish diversity: history of knowledge and discovery (Pisces). Zootaxa(2525):19-50.

Escoufier Y. 1973. Le traitement des variables vectorielles. Biometrics 29(4):751-760.
Esteve-Altava B. 2016. In search of morphological modules: A systematic review. Biological Reviews 92(3):1332-1347.
Eytan RI, Evans BR, Dornburg A, Lemmon AR, Lemmon EM, Wainwright PC, Near TJ. 2015. Are 100 enough? Inferring acanthomorph teleost phylogeny using Anchored Hybrid Enrichment. BMC Evolutionary Biology 15:20.
Faircloth BC, Sorenson L, Santini F, Alfaro ME. 2013. A phylogenomic perspective on the radiation of ray-finned fishes based upon targeted sequencing of ultraconserved elements (UCEs). PLoS One 8(6):7.
Farias IP, Orti G, Sampaio I, Schneider H, Meyer A. 1999. Mitochondrial DNA phylogeny of the family Cichlidae: Monophyly and fast molecular evolution of the neotropical assemblage. Journal of Molecular Evolution 48(6):703-711.
Farias IP, Orti G, Sampaio I, Schneider H, Meyer A. 2001. The cytochrome *b* gene as a phylogenetic marker: The limits of resolution for analyzing relationships among cichlid fishes. Journal of Molecular Evolution 53(2):89-103.
Faustino M, Power DM. 1999. Development of the pectoral, pelvic, dorsal and anal fins in cultured sea bream. Journal of Fish Biology 54(5):1094-1110.
Felsenstein J. 1973. Maximum-likelihood estimation of evolutionary trees from continuous characters. American Journal of Human Genetics 25(5):471-492.
Felsenstein J. 1985. Phylogenies and the comparative method. American Naturalist 125(1):1-15.
Fernholm B. 1998. Hagfish systematics. In: Jørgensen JM, Lomholt JP, Weber RE, Malte H, editors. The Biology of Hagfishes. London: Chapman & Hall. p 33-44.
Ferraris C. 1999. Plotosidae. In: Carpenter KE, Niem VH, editors. FAO species identification guide for fishery purposes. The living marine ressources of the western Central Pacific. Volume 3. Batoid fishes, chimaeras and bony fishes part 1 (Elopidae to Linophrynidae). Rome, Italy: Food and Agriculture Organization of the United Nations. p 1880-1883.
Filleul A, Lavoué S. 2001. Basal teleosts and the question of elopomorph monophyly. Morphological and molecular approaches. Comptes Rendus de l'Académie des Sciences Série III-Sciences de la Vie 324(4):393-399.
Fink WL. 1985. Phylogenetic interrelationships of the stomiid fishes (Teleostei: Stomiiformes). Miscellaneous Publications of the Museum of Zoology, University of Michigan 171:1-127.
Fischer W, Bianchi G, (Eds.). 1984. FAO species identification sheets for fishery purposes. Western Indian Ocean (Fishing Area 51). Volumes 1-6.
Foote M. 1991. Morphological and taxonomic diversity in a clade's history: The blastoid record and stochastic simulations. Contributions from the Museum of Paleontology, The University of Michigan 28(6):101-140.
Foote M. 1992a. Paleozoic record of morphological diversity in blastozoan echinoderms. Proceedings of the National Academy of Sciences of the United States of America 89:7325-7329.

Foote M. 1992b. Rarefaction analysis of morphological and taxonomic diversity. Paleobiology 18(1):1-16.
Foote M. 1993a. Contributions of individual taxa to overall morphological disparity. Paleobiology 19(4):403-419.
Foote M. 1993b. Discordance and concordance between morphological and taxonomic diversity. Paleobiology 19(2):185-204.
Foote M. 1994. Morphological disparity in Ordovician-Devonian crinoids and the early saturation of morphological space. Paleobiology 20(3):320-344.
Foote M. 1995. Morphological diversification of Paleozoic crinoids. Paleobiology 21(3):273-299.
Foote M. 1997. The evolution of morphological diversity. Annual Review of Ecology and Systematics 28:129-152.
Foote M. 1999. Morphological diversity in the evolutionary radiation of Paleozoic and post-Paleozoic crinoids. Paleobiology 25(2):1-115.
Forey P, Janvier P. 1993. Agnathans and the origin of jawed vertebrates. Nature 361(6408):129-134.
Forey P, Janvier P. 1994. Evolution of the early vertebrates. American Scientist 82(6):554-565.
Forey PL. 1984. Yet more reflections on agnathan-gnathostome relationships. Journal of Vertebrate Paleontology 4(3):330-343.
Forey PL. 1995. Agnathans recent and fossil, and the origin of jawed vertebrates. Reviews in Fish Biology and Fisheries 5(3):267-303.
Forey PL. 1998. History of the Coelacanth Fishes. London, UK: Chaman & Hall. 419 p.
Forey PL, Gardiner BG. 1986. Observations on *Ctenurella* (Ptyctodontida) and the classification of placoderm fishes. Zoological Journal of the Linnean Society 86(1):43-74.
Fowler HW. 1941. Contributions to the biology of the Philippine Archipelago and adjacent regions. The fishes of the groups Elasmobranchii, Holocephali, Isospondyli, and Ostariophysi obtained by the United States Bureau of Fisheries steamer "Albatross" in 1907 to 1910, chiefly in the Philippine Islands and ajacent seas. Bulletin of the United States National Museum 13(100):1-879.
Franchina CR, Hopkins CD. 1996. The dorsal filament of the weakly electric Apteronotidae (Gymnotiformes; Teleostei) is specialized for electroreception. Brain Behavior and Evolution 47(4):165-178.
Franklin O, Palmer C, Dyke G. 2014. Pectoral fin morphology of batoid fishes (Chondrichthyes: Batoidea): Explaining phylogenetic variation with geometric morphometrics. Journal of Morphology 275(10):1173-1186.
Freitas R, Gómez-Skarmeta JL, Rodrigues PN. 2014. New frontiers in the evolution of fin development. Journal of Experimental Zoology Part B-Molecular and Developmental Evolution 322B(7):540-552.
Freitas R, Zhang GJ, Cohn MJ. 2006. Evidence that mechanisms of fin development evolved in the midline of early vertebrates. Nature 442(7106):1033-1037.

Freitas R, Zhang GJ, Cohn MJ. 2007. Biphasic *Hoxd* gene expression in shark paired fins reveals an ancient origin of the distal limb domain. PLoS One 2(8):e754.

Friedman M. 2007. *Styloichthys* as the oldest coelacanth: Implications for early osteichthyan interrelationships. Journal of Systematic Palaeontology 5(3):289-343.

Friedman M. 2010. Postcranial evolution in early lungfishes (Dipnoi: Sarcopterygii): New insights from *Soederberghia groenlandica*. In: Elliott DK, Maisey JG, Yu X, Miao D, editors. Morphology, Phylogeny and Paleobiogeography of Fossil Fishes. München, Germany: Verlag Dr. Friedrich Pfeil. p 299-324.

Friedman M, Coates MI, Anderson P. 2007. First discovery of a primitive coelacanth fin fills a major gap in the evolution of lobed fins and limbs. Evolution & Development 9(4):329-337.

Friedman M, Johanson Z, Harrington RC, Near TJ, Graham MR. 2013a. An early fossil remora (Echeneoidea) reveals the evolutionary assembly of the adhesion disc. Proceedings of the Royal Society B-Biological Sciences 280(1766):7.

Friedman M, Keck BP, Dornburg A, Eytan RI, Martin CH, Hulsey CD, Wainwright PC, Near TJ. 2013b. Molecular and fossil evidence place the origin of cichlid fishes long after Gondwanan rifting. Proceedings of the Royal Society B-Biological Sciences 280(1770):1-8.

Froese R, Pauly D. 2016. Fishbase.

Fulcher BA, Motta PJ. 2006. Suction disk performance of echeneid fishes. Canadian Journal of Zoology 84(1):42-50.

Gabbott SE, Aldridge RJ, Theron JN. 1995. A giant conodont with preserved muscle tissue from the Upper Ordovician of South Africa. Nature 374(6525):800-803.

Gagnier P-Y. 1989. The oldest vertebrate: A 470-million-year-old jawless fish , *Sacabambaspis janvieri*, from the Ordovician of Bolivia. National Geographic Research 5(2):250-253.

Gagnier P-Y. 1993a. *Sacabambaspis janvieri*, vertébré ordovicien de Bolivie. 1. Analyse morphologique. Annales de Paléontologie 79(1):19-51.

Gagnier P-Y. 1993b. *Sacabambaspis janvieri*, vertébré ordovicien de Bolivie. 2. Analyse phylogénétique. Annales de Paléontologie 79(2):119-166.

Gagnier P-Y, Blieck A. 1992. On *Sacabambaspis janvieri* and the vertebrate diversity in Ordvician seas. In: Mark-Kurik E, editor. Fossil Fishes as Living Animals. Tallinn, Estonia: Academy of Sciences of Estonia. p 9-20.

Gagnier P-Y, Blieck ARM, Rodrigo GS. 1986. First Ordovician vertebrate from South America. Geobios 19(5):629-634.

Gagnier P-Y, Hanke GF, Wilson MVH. 1999. *Tetanopsyrus lindoei* gen. et sp. nov., an Early Devonian acanthodian from the Northwest Territories, Canada. Acta Geologica Polonica 49(2):81-96.

Gagnier P-Y, Wilson MVH. 1996. Early Devonian acanthodians from northern Canada. Palaeontology 39:241-258.

Gai Z-K, Zhu M, Zhao W-J. 2005. New material of eugaleaspids from the Silurian of Changxing, Zhejiang, China, with a discussion on the eugaleaspid phylogeny. Vertebrata Palasiatica 43(1):61-75.

Gai ZK, Donoghue PCJ, Zhu M, Janvier P, Stampanoni M. 2011. Fossil jawless fish from China foreshadows early jawed vertebrate anatomy. Nature 476(7360):324-327.

Gans C. 1975. Tetrapod limblessness: Evolution and functional corollaries. American Zoologist 15(2):455-467.

Gardiner BG, Schaeffer B. 1989. Interrelationships of lower actinopterygian fishes. Zoological Journal of the Linnean Society 97(2):135-187.

Gardiner BG, Schaeffer B, Masserie JA. 2005. A review of the lower actinopterygian phylogeny. Zoological Journal of the Linnean Society 144(4):511-525.

Garman S. 1913. The Plagiostomia (Sharks, skates, and rays). Memoirs of the Museum of Comparative Zoology at Harvard College 36:1-515.

Garstang W. 1928. The morphology of the Tunicata, and its bearings on the phylogeny of the Chordata. Quarterly Journal of Microscopical Science 72:51-187.

Garstang W. 1931. The phyletic classification of Teleostei. Proceedings of the Leeds Philosophical and Literary Society, Scientific Section 2(5):240-260.

Gatesy J, Matthee C, DeSalle R, Hayashi C. 2002. Resolution of a supertree/supermatrix paradox. Systematic Biology 51(4):652-664.

Gatesy J, Springer MS. 2004. A critique of matrix representation with parsimony supertrees. In: Bininda-Emonds ORP, editor. Phylogenetic Supertrees - Combining Information to Reveal the Tree of Life. Dordrecht, Netherlands: Kluwer Academic Publishers. p 369-388.

Gayet M, Meunier FJ. 1991. Première découverte de Gymnotiformes fossiles (Pisces, Ostariophysi) dans le Myocène supérieur de Bolivie. Comptes Rendus de l'Académie des Sciences, Paris, Série 2 313:471-476.

Gayet M, Meunier FJ, Kirschbaum F. 1994. *Ellisella kirschbaumi* Gayet and Meunier, 1991, Gymnotiforme fossile de Bolivie et ses relations phylogénétiques au sein des formes actuelles. Cybium 18(3):273-306.

Gegenbaur C. 1876. Zur Morphologie der gliedmaassen der Wirbelthier. Morphologisches Jahrbuch 2:396-420.

Gerhart J, Kirschner M. 2007. The theory of facilitated variation. Proceedings of the National Academy of Sciences of the United States of America 104:8582-8589.

Germain D, Sanchez S, Janvier P, Tafforeau P. 2014. The presumed hagfish *Myxineidus gononorum* from the Upper Carboniferous of Montceau-les-Mines (Saone-et-Loire, France): New data obtained by means of propagation phase contrast X-ray synchrotron microtomography. Annales de Paléontologie 100(2):131-135.

Gess RW, Coates MI. 2015. High-latitude chondrichthyans from the Late Devonian (Famennian) Witpoort Formation of South Africa. Palaeontologische Zeitschrift 89(2):147-169.

Gess RW, Coates MI, Rubidge BS. 2006. A lamprey from the Devonian period of South Africa. Nature 443(7114):981-984.

Gibson-Brown JJ, Agulnik SI, Chapman DL, Alexiou M, Garvey N, Silver LM, Papaioannou VE. 1996. Evidence of a role for *T-box* genes in the evolution of limb morphogenesis and the specification of forelimb/hindlimb identity. Mechanisms of Development 56(1-2):93-101.

Giles S, Coates MI, Garwood RJ, Brazeau MD, Atwood R, Johanson Z, Friedman M. 2015a. Endoskeletal structure in *Cheirolepis* (Osteichthyes, Actinopterygii), an early ray-finned fish. Palaeontology 58(5):849-870.

Giles S, Darras L, Clement G, Blieck A, Friedman M. 2015b. An exceptionally preserved Late Devonian actinopterygian provides a new model for primitive cranial anatomy in ray-finned fishes. Proceedings of the Royal Society B-Biological Sciences 282(1816):10.

Giles S, Friedman M, Brazeau MD. 2015c. Osteichthyan-like cranial conditions in an Early Devonian stem gnathostome. Nature 520(7545):82-85.

Gill T. 1890. On the relations of Cyclopteroidea. Proceedings of the United States National Museum 13:361-376.

Gillis JA, Dahn RD, Shubin NH. 2009. Shared developmental mechanisms pattern the vertebrate gill arch and paired fin skeletons. Proceedings of the National Academy of Sciences of the United States of America 106(14):5720-5724.

Ginter M, Hampe O, Duffin C. 2010. Volume 3D - Chondrichthyes - Paleozoic Elasmobranchii: Teeth. Schultze H-P, editor. München, Germany: Verlag Dr. Friedrich Pfeil. 168 p.

Ginter M, Turner S. 2010. The middle Paleozoic selachian genus *Thrinacodus*. Journal of Vertebrate Paleontology 30(6):1666-1672.

Goodrich ES. 1906. Notes on the development, structure, and origin of the median and paired fins of fish. Quarterly Journal of Microscopical Science 50:333-376.

Goodrich ES. 1909. A Treatise on Zoology, Part IX: Vertebrata Craniata (First Fascicle: Cyclostomes and Fishes). London: Adam and Charles Black. 518 p.

Goodrich ES. 1930. Studies on the Structure and Development of Vertebrates. London, UK: McMillan and Co. 837 p.

Goodsir J. 1844. On the anatomy of *Amphioxus lanceolatus*; lancelet, Yarrell. Transactions of the Royal Society of Edinburgh 15(15):247-263.

Goodyear RH, Gibbs RH. 1986. Family No. 71: Malacosteidae. In: Smith MM, Heemstra PC, editors. Smith's Sea Fishes. Berlin, Germany: Springer-Verlag. p 235-236.

Gormon JR. 1986. Family No. 60: Plotosidae. In: Smith MM, Heemstra PC, editors. Smith's Sea Fishes. Berlin, Germany: Springer-Verlag. p 213-213.

Goswami A. 2006. Cranial modularity shifts during mammalian evolution. American Naturalist 168(2):270-280.

Goswami A, Polly PD. 2010. The influence of modularity on cranial morphological disparity in Carnivora and Primates (Mammalia). PLoS One 5(3):8.

Goswami A, Smaers JB, Soligo C, Polly PD. 2014. The macroevolutionary consequences of phenotypic integration: From development to deep time. Philosophical Transactions of the Royal Society B-Biological Sciences 369(1649):15.

Goswami A, Weisbecker V, Sánchez-Villagra MR. 2009. Developmental modularity and the marsupial-placental dichotomy. Journal of Experimental Zoology Part B-Molecular and Developmental Evolution 312B(3):186-195.

Goüan A. 1770. Histoire des poissons. Strasbourg: Amand König. 252 p.

Goujet D, Young GC. 1995. Interrelationships of placoderms revisited. Geobios M.S. 19:89-95.

Goujet D, Young GC. 2004. Placoderm anatomy and phylogeny: New insights. In: Arratia G, Wilson MVH, Cloutier R, editors. Recent Advances in the Origin and Early Radiation of Vertebrates. Munich, Germany: Verlag Dr. Friedrich Pfeil p109-126.

Gould SJ. 1977. Ontogeny and Phylogeny. Cambridge, UK: Harvard University Press. 501 p.

Gould SJ. 1989. Wonderful Life: The Burgess Shale and the Nature of History. New York, NY: W. W. Norton and Company, Inc. 347 p.

Grande L, Bemis WE. 1998. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. Supplement of the Journal of Vertebrate Paleontology Memoir 4 18:1-696.

Grandel H, Schulte-Merker S. 1998. The development of the paired fins in the zebrafish (*Danio rerio*). Mechanisms of Development 79(1-2):99-120.

Gray JE. 1831. XIII. Description of twelve new genera of fish, discoveres by Gen. Hardwicke, in India, the greater part in the British Museum. The Zoological Miscellany 1:7-9.

Green WDK. 1996. The thin-plate spline and images with curving features. In: Mardia KV, Gill CA, Dryden IL, editors. Proceedings in Image Fusion and Shape Variability Techniques. Leeds, UK: Leeds University Press. p 79-87.

Greenwood PH, Rosen DE, Weitzman SH, Myers GS. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bulletin of the American Museum of Natural History 131(4):339-456.

Gregory WK, Raven HC. 1941. Studies on the origin and early evolution of paired fins and limbs. 1. Paired fins and girdles in ostracoderms, placoderms and other primitive fishes. Annals of the New York Academy of Science 42:275-291.

Grogan ED, Lund R. 2000. *Debeerius ellefseni* (fam. nov., gen. nov., spec. nov.), an autodiastylic chondrichthyan from the Mississippian Bear Gulch Limestone of Montana (USA), the relationships of the Chondrichthyes, and comments on gnathostome evolution. Journal of Morphology 243(3):219-245.

Grogan ED, Lund R. 2004. The origin and relationships of early Chondrichthyes. In: Carrier JC, Musick JA, Heithaus MR, editors. Biology of Sharks and Their Relatives. Boca Raton: CRC Press. p 3-31.

Grogan ED, Lund R. 2008. A basal elasmobranch, *Thrinacoselache gracia* n. gen. & sp., (Thrinacodontidae, new family) from the Bear Gulch Limestone, Serpukhovian of Montana, USA. Journal of Vertebrate Paleontology 28(4):970-988.

Grogan ED, Lund R. 2009. Two new iniopterygians (Chondrichthyes) from the Mississippian (Serpukhovian) Bear Gulch Limestone of Montana with evidence of a new form of chondrichthyan neurocranium. Acta Zoologica 90:134-151.

Grogan ED, Lund R, Greenfest-Allen E. 2012. The origin and relationships of early chondrichthyans. In: Carrier JC, Musick JA, Heithaus MR, editors. Biology of Sharks and their Relatives, Second Edition. Boca Raton, FL: CRC Press. p 3-29.

Grünbaum T, Cloutier R, Vincent B. 2012. Dynamic skeletogenesis in fishes: Insight of exercise training on developmental plasticity. Developmental Dynamics 241(10):1507-1524.

Günther ACLG. 1880. An Introduction to the Study of Fishes. Edinburgh: Adam and Charles Black. 720 p.

Hadzhiev Y, Lele Z, Schindler S, Wilson SW, Ahlberg P, Strahle U, Muller F. 2007. Hedgehog signaling patterns the outgrowth of unpaired skeletal appendages in zebrafish. BMC Developmental Biology 7:12.

Hairapetian V, Valiukevičius J, Burrow CJ. 2006. Early Frasnian acanthodians from central Iran. Acta Palaeontologica Polonica 51(3):499-520.

Hall BK. 1995. Homology and embryonic development. Evolutionary Biology 28:1-37.

Hall BK. 2010. Charles Darwin, embryology, evolution and skeletal plasticity. Journal of Applied Ichthyology 26(2):148-151.

Hallgrímsson B, Jamniczky H, Young NM, Rolian C, Parsons TE, Boughner JC, Marcucio RS. 2009. Deciphering the palimpsest: Studying the relationship between morphological integration and phenotypic covariation. Evolutionary Biology 36(4):355-376.

Hallgrímsson B, Willmore K, Hall BK. 2002. Canalization, developmental stability, and morphological integration in primate limbs. Yearbook of Physical Anthropology 45:131-158.

Halstead BW. 1978. Chapter XVIII - Vertebrates. Class Chondrichthyes. Poisonous and Venomous Marine Animals of the World. Princeton, NJ: Darwin Press. p 605-678.

Halstead BW, Ocampo RR, Modglin FR. 1955. A study on the comparative anatomy of the venom apparatus of certain North American stingrays. Journal of Morphology 97(1):1-21.

Halstead LB. 1973. The heterostracan fishes. Biological Reviews 48:279-332.

Halstead LB. 1982. Evolutionary trends and the phylogeny of the Agnatha. In: Joysey KA, Friday AE, editors. Problems of Phylogenetic Reconstruction. London, UK: Academic Press. p 159-196.

Halstead LB, Turner S. 1973. Silurian and Devonian ostracoderms. In: Hallam A, editor. Atlas of Palaeobiogeography. Amsterdam, Netherlands: Elsevier Scientific Publishing Company. p 67-79.

Hanke GF. 2002. *Paucicanthus vanelsti* gen. et sp. nov., an Early Devonian (Lochkovian) acanthodian that lacks paired fin-spines. Canadian Journal of Earth Sciences 39(7):1071-1083.

Hanke GF. 2008. *Promesocanthus eppleri* n. gen., n. sp., a mesacanthid (Acanthodii, Acanthodiformes) from the Lower Devonian of northern Canada. Geodiversitas 30(2):287-302.

Hanke GF, Davis SP. 2008. Redescription of the acanthodian *Gladiobranchus probaton* Bernacsek & Dineley, 1977, and comments on diplacanthid relationships. Geodiversitas 30(2):303-330.

Hanke GF, Davis SP, Wilson MVH. 2001. New species of the acanthodian genus *Tetanopsyrus* from Northern Canada, and comments on related taxa. Journal of Vertebrate Paleontology 21(4):740-753.

Hanke GF, Davis SR. 2012. A re-examination of *Lupopsyrus pygmaeus* Bernacsek & Dineley, 1977 (Pisces, Acanthodii). Geodiversitas 34(3):469-487.

Hanke GF, Wilson MVH. 2002. New teleostome fishes and acanthodian systematics. Journal of Vertebrate Paleontology 22(3):62A.

Hanke GF, Wilson MVH. 2004. New teleostome fishes and acanthodian systematics. In: Arratia G, Wilson MVH, Cloutier R, editors. Recent Advances in the Origin and Early Radiation of Vertebrates. München, Germany: Verlag Dr. Friedrich Pfeil. p 189-216.

Hanke GF, Wilson MVH. 2006. Anatomy of the Early Devonian acanthodian *Brochoadmones milesi* based on nearly complete body fossils, with comments on the evolution and development of paired fins. Journal of Vertebrate Paleontology 26(3):526-537.

Hanke GF, Wilson MVH. 2010. The putative stem-group chondrichthyans *Kathemacanthus* and *Seretolepis* from the Lower Devonian MOTH locality, Mackenzie Mountains, Canada. In: Elliott DK, Maisey JG, Yu X, Miao D, editors. Morphology, Phylogeny and Paleobiogeography of Fossil Fishes. München, Germany: Verlag Dr. Friedrich Pfeil. p 159-182.

Hansen TF. 1997. Stabilizing selection and the comparative analysis of adaptation. Evolution 51(5):1341-1351.

Hansen TF. 2003. Is modularity necessary for evolvability? Remarks on the relationship between pleiotropy and evolvability. Biosystems 69(2-3):83-94.

Hansen TF. 2006. The evolution of genetic architecture. Annual Review of Ecology Evolution and Systematics 37:123-157.

Hansen TF, Armbruster WS, Carlson ML, Pelabon C. 2003. Evolvability and genetic constraint in *Dalechampia* blossoms: Genetic correlations and conditional evolvability. Journal of Experimental Zoology Part B-Molecular and Developmental Evolution 296B(1):23-39.

Hansen TF, Houle D. 2008. Measuring and comparing evolvability and constraint in multivariate characters. Journal of Evolutionary Biology 21(5):1201-1219.

Hardisty MW. 1979. Biology of the Cyclostomes. London: Chapman and Hall. 428 p.

Hardisty MW, Potter IC. 1971. The general biology of adult lampreys. In: Hardisty MW, Potter IC, editors. The Biology of Lampreys. Volume 1. London, UK: Academic Press. p 127-206.

Harmon LJ, Losos JB, Davies TJ, Gillespie RG, Gittleman JL, Jennings WB, Kozak KH, McPeek MA, Moreno-Roark F, Near TJ and others. 2010. Early bursts of body size and shape evolution are rare in comparative data. Evolution 64(8):2385-2396.

Harmon LJ, Schulte JA, Larson A, Losos JB. 2003. Tempo and mode of evolutionary radiation in iguanian lizards. Science 301(5635):961-964.

Harrell FE. 2016. Hmisc: Harrell Miscellaneous R package version 3.17-4.

Harris JE. 1936. The role of the fins in the equilibrium of the swimming fish. I. Wind-tunnel tests on a model of *Mustelus canis* (Mitchill). Journal of Experimental Biology 13(4):476-493.

Harris JE. 1938. The role of the fins in the equilibrium of the swimming fish. II. The role of the pelvic fins. Journal of Experimental Biology 15(1):32-47.

Harvey PH, Pagel MD. 1991. The Comparative Method in Evolutionary Biology. Oxford, UK: Oxford University Press. 239 p.

He SP, Mayden RL, Wang XZ, Wang W, Tang KL, Chen WJ, Chen YY. 2008. Molecular phylogenetics of the family Cyprinidae (Actinopterygii : Cypriniformes) as evidenced by sequence variation in the first intron of S7 ribosomal protein-coding gene: Further evidence from a nuclear gene of the systematic chaos in the family. Molecular Phylogenetics and Evolution 46(3):818-829.

Hedges SB. 2001. Molecular evidence for the early history of living vertebrates. In: Ahlberg PE, editor. Major Events in Early Vertebrate Evolution: Palaeontology, Phylogeny, Genetics and Development. London: Taylor & Francis. p 119-134.

Heidtke U. 1990. Studien über *Acanthodes* (Pisces: Acanthodii) aus dem saar-pfälzischen Rotliegend (?Ober-Karbon-Unter-Perm, SW-Deutschland). In: Heidtke U, editor. New Research on Permo-Carboniferous Fauna. Pollichia-Buch Nr. 19. Bad Dürkheim: Pfalzmuseum für Naturkunde. p 1-86.

Heimberg AM, Cowper-Sallari R, Semon M, Donoghue PCJ, Peterson KJ. 2010. microRNAs reveal the interrelationships of hagfish, lampreys, and gnathostomes and the nature of the ancestral vertebrate. Proceedings of the National Academy of Sciences of the United States of America 107(45):19379-19383.

Heintz A. 1931. Revision of the structure of *Coccosteus decipiens* Ag. Norsk Geologisk Tidsskrift 12:291-313.

Heintz A. 1938. Notes on Arthrodira. Norsk Geografisk Tidsskrift 18:1-27.

Heintz A. 1939. Cephalaspids from the Downtonian of Norway. NorskeVidenskapsakademiens Skrifter (Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo): Matematiske-Naturvetenskapslige Klasse 5:1-119.

Heintz A. 1967. A new trematapidid from Ringerike, South Norway. Journal of the Linnean Society of London, Zoology 47(311):55-68.

Hendrikse JL, Parsons TE, Hallgrímsson B. 2007. Evolvability as the proper focus of evolutionary developmental biology. Evolution & Development 9(4):393-401.

Herdman WA. 1904. Ascidians and amphioxus. In: Harmer SF, Shipley AE, editors. The Cambridge Natural History. Volume VII. London, UK: McMillan and Co. Limited. p 35-138.

Hinchliffe JR, Vorobyeva EI, Géraudie J. 2001. Is there a tetrapod developmental *Bauplan* underlying limb evolution? Evidence from a teleost fish and from urodele and anuran amphibians. In: Ahlberg PE, editor. Major Events in Early Vertebrate Evolution: Palaeontology, Phylogeny, Genetics and Development. London: Taylor & Francis. p 377-391.

Holland ND, Chen JY. 2001. Origin and early evolution of the vertebrates: New insights from advances in molecular biology, anatomy, and palaeontology. Bioessays 23(2):142-151.

Holland ND, Holland LZ. 1991. The histochemistry and fine structure of the nutritional reserves in the fin rays of a lancelet, *Branchiostoma lanceolatum* (Cephalochordata, Acrania). Acta Zoologica 72(4):203-207.

Holland T, Long JA. 2009. On the phylogenetic position of *Gogonasus andrewsae* Long 1985, within the Tetrapodomorpha. Acta Zoologica 90:285-296.

Hollò G, Novàk M. 2012. The manoeuvrability hypothesis to explain the maintenance of bilateral symmetry in animal evolution. Biology Direct 7(22).

Hopson JA. 1974. The functional significance of the hypocercal tail and lateral fin fold of anaspid ostracoderms. Fieldiana, Geology 33(5):83-93.

Hou XG, Aldridge RJ, Siveter DJ, Feng XH. 2002. New evidence on the anatomy and phylogeny of the earliest vertebrates. Proceedings of the Royal Society of London Series B-Biological Sciences 269(1503):1865-1869.

Hou XG, Ramskold L, Bergstrom J. 1991. Composition and preservation of the Chengjiang fauna - A Lower Cambrian soft-bodied biota. Zoologica Scripta 20(4):395-411.

Hounsfield GN. 1973. Computerized transverse axial scanning (tomography): Part I. Description of system. British Journal of Radiology 46(552):1016-1022.

Howell AB. 1933. Homology of the paired fins in fishes. Journal of Morphology 54(3):451-457.

Hubbs CL. 1922. A list of the lancelets of the world with diagnoses of five new species of *Branchiostoma*. Occasional Papers of the Museum of Zoology, University of Michigan 105:1-16.

Hulley PA. 1986. Family No. 70: Idiacanthidae. In: Smith MM, Heemstra PC, editors. Smith's Sea Fishes. Berlin, Germany: Springer-Verlag. p 234-235.

Human BA, Owen EP, Compagno LJV, Harley EH. 2006. Testing morphologically based phylogenetic theories within the cartilaginous fishes with molecular data, with special reference to the catshark family (Chondrichthyes; Scyliorhinidae) and the interrelationships within them. Molecular Phylogenetics and Evolution 39(2):384-391.

Hume JB, Bean CW, Adams CE. 2014. Morphological abnormalities in a population of *Lampetra planeri*, with a short review of petromyzontid teratologies. Journal of Fish Biology 84(5):1614-1619.

Hurley IA, Mueller RL, Dunn KA, Schmidt EJ, Friedman M, Ho RK, Prince VE, Yang ZH, Thomas MG, Coates MI. 2007. A new time-scale for ray-finned fish evolution. Proceedings of the Royal Society B-Biological Sciences 274(1609):489-498.

Huxley TH. 1871. A Manual of the Anatomy of Vertebrated Animals. London: J. & A. Churchill. 510 p.

Inoue JG, Kumazawa Y, Miya M, Nishida M. 2009. The historical biogeography of the freshwater knifefishes using mitogenomic approaches: A Mesozoic origin of the Asian notopterids (Actinopterygii: Osteoglossomorpha). Molecular Phylogenetics and Evolution 51(3):486-499.

Inoue JG, Miya M, Lam K, Tay BH, Danks JA, Bell J, Walker TI, Venkatesh B. 2010. Evolutionary origin and phylogeny of the modern holocephalans (Chondrichthyes: Chimaeriformes): A mitogenomic perspective. Molecular Biology and Evolution 27(11):2576-2586.

Inoue JG, Miya M, Tsukamoto K, Nishida M. 2001. A mitogenomic perspective on the basal teleostean phylogeny: Resolving higher-level relationships with longer DNA sequences. Molecular Phylogenetics and Evolution 20(2):275-285.

Inoue JG, Miya M, Tsukamoto K, Nishida M. 2003. Basal actinopterygian relationships: A mitogenomic perspective on the phylogeny of the "ancient fish". Molecular Phylogenetics and Evolution 26(1):110-120.

Inoue JG, Miya M, Tsukamoto K, Nishida M. 2004. Mitogenomic evidence for the monophyly of elopomorph fishes (Teleostei) and the evolutionary origin of the leptocephalus larva. Molecular Phylogenetics and Evolution 32(1):274-286.

Insom E, Pucci A, Simonetta AM. 1995. Cambrian Protochordata, their origin and significance. Bollettino Di Zoologia 62(3):243-252.

Isaac A, Rodriguez-Esteban C, Ryan A, Altabef M, Tsukui T, Patel K, Tickle C, Izpisua-Belmonte JC. 1998. *Tbx* genes and limb identity in chick embryo development. Development 125(10):1867-1875.

Ishiguro NB, Miya M, Nishida M. 2003. Basal euteleostean relationships: A mitogenomic perspective on the phylogenetic reality of the "Protacanthopterygii". Molecular Phylogenetics and Evolution 27(3):476-488.

Janvier P. 1978. Les nageoires paires des ostéostracés et la position systématique des céphalaspidomorphes. Annales de Paléontologie (Vertébrés) 64(2):113-142.

Janvier P. 1981a. *Norselaspis glacialis* n.g., n.sp. et les relations phylogénétiques entre les Kieraspidiens (Osteostraci) du Dévonien inférieur du Spitsberg. Palaeovertebrata 11(2-3):19-131.

Janvier P. 1981b. The phylogeny of the Craniata, with particular reference to the significance of fossil "agnathans". Journal of Vertebrate Paleontology 1(2):121-159.

Janvier P. 1984. The relationships of the Osteostraci and Galeaspida. Journal of Vertebrate Paleontology 4(3):344-358.

Janvier P. 1985a. Environmental framework of the diversification of the Osteostraci during the Silurian and Devonian. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 309(1138):259-272.

Janvier P. 1985b. Les thyestidiens (Osteostraci) du Silurien de Saaremaa (Estonie). Deuxième partie : Analyse phylogénétique, répartition stratigraphique, remarques sur les genres *Auchenaspis*, *Timanaspis*, *Tyriaspis*, *Didymaspis*, *Sclerodus* et *Tannuaspis*. Annales de Paléontologie 71(3):187-216.

Janvier P. 1985c. Preliminary description of Lower Devonian Osteostraci from Podolia (Ukrainian U.S.S.R.). Bulletin of the British Museum (Natural History) - Geology 38(5):309-334.

Janvier P. 1987. The paired fins of anaspids: One more hypothesis about their function. Journal of Paleontology 61(4):850-853.

Janvier P. 1996a. The dawn of the vertebrates: Characters versus common ascent in the rise of current vertebrate phylogenies. Palaeontology 39:259-287.

Janvier P. 1996b. Early Vertebrates. Oxford, UK: Oxford University Press. 393 p.

Janvier P. 1996c. The Miguasha "Anaspida". In: Schultze H-P, Cloutier R, editors. Devonian Fishes and Plants of Miguasha, Quebec, Canada. München, Germany: Verlag Dr. Friedrich Pfeil. p 134-140.

Janvier P. 2003. Vertebrate characters and the Cambrian vertebrates. Comptes Rendus Palevol 2(6-7):523-531.

Janvier P. 2007. Homologies and evolutionary transitions in early vertebrate history. In: Anderson JS, Sues HD, editors. Major Transitions in Vertebrate Evolution. Bloomington: Indiana University Press. p 57-121.

Janvier P. 2008. Early jawless vertebrates and cyclostome origins. Zoological Science 25(10):1045-1056.

Janvier P, Arsenault M. 1996. Osteostraci. In: Schultze H-P, Cloutier R, editors. Devonian Fishes and Plants of Miguasha, Quebec, Canada. München, Germany: Verlag Dr. Friedrich Pfeil. p 123-133.

Janvier P, Arsenault M. 2007. The anatomy of *Euphanerops longaevus* Woodward, 1900, an anaspid-like jawless vertebrate from the Upper Devonian of Miguasha, Quebec, Canada. Geodiversitas 29(1):143-216.

Janvier P, Arsenault M, Desbiens S. 2004a. Calcified cartilage in the paired fins of the osteostracan *Escuminaspis laticeps* (Traquair 1880), from the Late Devonian of Miguasha (Quebec, Canada), with a consideration of the early evolution of the

pectoral fin endoskeleton in vertebrates. Journal of Vertebrate Paleontology 24(4):773-779.

Janvier P, Blieck A. 1979. New data on the internal anatomy of the Heterostraci (Agnatha), with general remarks on the phylogeny of the Craniota. Zoologica Scripta 8:287-296.

Janvier P, Desbiens S, Willett JA, Arsenault M. 2006. Lamprey-like gills in a gnathostome-related Devonian jawless vertebrate. Nature 440(7088):1183-1185.

Janvier P, Lund R. 1983. *Hardistiella montanensis* n. gen. et sp. (Petromyzontida) from the Lower Carboniferous of Montana, with remarks on the affinities of the lampreys. Journal of Vertebrate Paleontology 2(4):407-413.

Janvier P, Lund R, Grogan ED. 2004b. Further consideration of the earliest known lamprey, *Hardistiella montanensis* Janvier and Lund, 1983, from the Carboniferous of Bear Gulch, Montana, USA. Journal of Vertebrate Paleontology 24(3):742-743.

Jarvik E. 1959. Dermal fin-rays and Holmgren's principle of delamination. Kunglica Svenska Vetenskapsakademiens Handlingar 6(1):3-51.

Jarvik E. 1960. Théories de l'évolution des vertébrés reconsidérées à la lumière des récentes découvertes sur les vertébrés inférieurs. Paris: Masson et Cie, Libraires de L'Académie de Médicine. 104 p.

Jayaram KC. 1981. The Freshwater Fishes of India, Pakistan, Bangladesh, Burma and Sri Lanka. Calcutta, India: Zoological Survey of India. 475 p.

Jayaram KC. 1982. Aid to the identification of the siluroid fishes of India, Burma, Sri Lanka, Pakistan and Bangladesh. 5. Ariidae and Plotosidae. Records of the Zoological Survey of India. Miscellaneous publications Occasional paper No. 37:1-41.

Jefferies RPS. 1973. The Ordovician fossil *Lagynocystis pyramidalis* (Barrande) and the ancestry of *Amphioxus*. Philosophical Transactions of the Royal Society B-Biological Sciences 265(871):409-469.

Jefferies RPS. 1979. The origin of the chordates - A methodological essay. In: House MR, editor. The Origin of Major Invertebrate Groups. London, UK: Academic Press. p 443-477.

Jefferies RPS. 1986. The Ancestry of the Vertebrates. Cambridge, UK: Cambridge University Press. 376 p.

Jefferies RPS, Lewis DN. 1978. The English Silurian fossil *Placocystites forbesianus* and the ancestry of the vertebrates. Philosophical Transactions of the Royal Society B-Biological Sciences 282(990):205-323.

Jessen HL. 1966. Die Crossopterygier des Oberen Plattenkalkes (Devon) der Bergisch-Gladbach-Paffrather Mulde (Rheinisches Schiefergebirge) unter Berücksichtigung von amerikanischem und europäischem *Onychodus*-material. Arkiv för Zoologi 18:305-389.

Johanson Z. 1997. New *Remigolepis* (Placodermi; Antiarchi) from Canowindra, New South Wales, Australia. Geological Magazine 134(6):813-846.

Johanson Z. 2002. Vascularization of the osteostracan and antiarch (Placodermi) pectoral fin: Similarities, and implications for placoderm relationships. Lethaia 35(2):169-186.

Johanson Z. 2010. Evolution of paired fins and the lateral somitic frontier. Journal of Experimental Zoology Part B-Molecular and Developmental Evolution 314B(5):347-352.

Johanson Z, Ahlberg PE. 2001. Devonian rhizodontids and tristichopterids (Sarcopterygii; Tetrapodomorpha) from East Gondwana. Transactions of the Royal Society of Edinburgh-Earth Sciences 92:43-74.

Johanson Z, Ericsson R, Long J, Evans F, Joss J. 2009. Development of the axial skeleton and median fin in the Australian lungfish, *Neoceratodus forsteri*. The Open Zoology Journal 2:91-101.

Johanson Z, Long JA, Talent JA, Janvier P, Warren JW. 2006. Oldest coelacanth, from the Early Devonian of Australia. Biology Letters 2(3):443-446.

Johansson PKE, Douglass TG, Lowe CG. 2004. Caudal spine replacement and histogenesis in the round stingray, *Urobatis halleri*. Bulletin of the Southern California Academy of Science 103(3):115-124.

Johnson GD, Britz R. 2005. Leis' conundrum: Homology of the clavus of the ocean sunfishes. 2. Ontogeny of the median fins and axial skeleton of *Ranzania laevis* (Teleostei, Tetraodontiformes, Molidae). Journal of Morphology 266(1):11-21.

Johnson GD, Patterson C. 1993. Percomorph phylogeny: A survey of acanthomorphs and a new proposal. Bulletin of Marine Science 52(1):554-626.

Jordan DS, Evermann BW. 1896. The fishes of North and Middle America: Descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. Part I. Bulletin of the United States National Museum 47:1-1240.

Jordan DS, Gilbert CH. 1882. Synopsis of the fishes of North America. Bulletin of the United States National Museum 16:1-1018.

Jordan DS, Snyder JO. 1901. A review of the lancelets, hag-fishes, and lampreys of Japan, with description of two new species. Proceedings of the United States National Museum 23(1233):725-734.

Joss J, Longhurst T. 2001. Lungfish paired fins. In: Ahlberg PE, editor. Major Events in Early Vertebrate Evolution: Palaeontology, Phylogeny, Genetics and Development. London: Taylor & Francis. p 370-376.

Jousselin E, Genson G, Coeur d'Acier A. 2010. Evolutionary lability of a complex life cycle in the aphid genus *Brachycaudus*. BMC Evolutionary Biology 10(295):1-15.

Kaup JJ. 1856. Catalogue of Apodal Fish, in the Collection of the British Museum. London, UK: British Museum of Natural History. 163 p.

Kawaguchi K, Moser HG. 1984. Stomiatoidea: Development. In: Moser HG, Richards WJ, Cohen DM, Fahay MP, Kendall AW, Richardson SL, editors. Ontogeny and Systematics of Fishes. Based on an international symposium dedicated to

the memory of Elbert Halvor Ahlstrom. Lawrence, KS: The American Society of Ichthyologists and Herpetologists. p 169-181.

Kawahara R, Miya M, Mabuchi K, Lavoué S, Inoue JG, Satoh TP, Kawaguchi A, Nishida M. 2008. Interrelationships of the 11 gasterosteiform families (sticklebacks, pipefishes, and their relatives): A new perspective based on whole mitogenome sequences from 75 higher teleosts. Molecular Phylogenetics and Evolution 46(1):224-236.

Keating JN, Donoghue PCJ. 2016. Histology and affinity of anaspids, and the early evolution of the vertebrate dermal skeleton. Proceedings of the Royal Society B-Biological Sciences 283(1826):20152917.

Keating JN, Sansom RS, Purnell MA. 2012. A new osteostracan fauna from the Devonian of the Welsh Borderlands and observations on the taxonomy and growth of Osteostraci. Journal of Vertebrate Paleontology 32(5):1002-1017.

Kemp A. 2002a. Amino acid residues in conodont elements. Journal of Paleontology 76(3):518-528.

Kemp A. 2002b. Hyaline tissue of thermally unaltered conodont elements and the enamel of vertebrates. Alcheringa 26(1-2):23-36.

Kemp A, Nicoll RS. 1995. Protochordate affinities of conodonts. CFS Courier Forschunginstitut Senckenberg 182:235-245.

Kemp A, Nicoll RS. 1996. A histochemical analysis of biological residues in conodont elements. Modern Geology 20(3-4):287-302.

Kemp NE. 1999. Integumentary system and teeth. In: Hamlett WC, editor. Sharks, Skates and Rays: The Biology of Elasmobranch Fishes. Baltimore, Maryland: The Johns Hopkins University Press. p 43-68.

Kenaley CP, Hartel KE. 2005. A revision of Atlantic species of *Photostomias* (Teleostei: Stomiidae: Malacosteinae), with a description of a new species. Ichthyological Research 52(3):251-263.

Khonsari RH, Li B, Vernier P, Northcutt RG, Janvier P. 2009. Agnathan brain anatomy and craniate phylogeny. Acta Zoologica 90:52-68.

Kiaer J. 1911. A new Downtonian fauna in the sandstone series of the Kristiania area: A preliminary report. Videnskapsselskapets Skrifter. I. Matematiske-Naturvidenskaplige Klasse(7):1-22.

Kiaer J. 1924. The Downtonian fauna of Norway. I. Anaspida, with a geological introduction. Videnskapsselskapets Skrifter. I. Matematiske-Naturvidenskaplige Klasse(6):1-139.

Kirkaldy JW. 1895. A revision of the genera and species of the Branchiostomidae. Quarterly Journal of Microscopical Science 37:303-323.

Kirschner M, Gerhart J. 1998. Evolvability. Proceedings of the National Academy of Sciences of the United States of America 95(15):8420-8427.

Kitamura T, Takemura A, Watabe S, Taniuchi T, Shimizu M. 1996. Molecular phylogeny of the sharks and rays of superorder Squalea based on mitochondrial cytochrome b gene. Fisheries Science 62(3):340-343.

Klimley AP. 2013. The Biology of Sharks and Rays. Chicago, IL: The University of Chicago Press. 512 p.

Klingenberg CP. 2008. Morphological integration and developmental modularity. Annual Review of Ecology Evolution and Systematics 39:115-132.

Klingenberg CP. 2009. Morphometric integration and modularity in configurations of landmarks: Tools for evaluating *a priori* hypotheses. Evolution & Development 11(4):405-421.

Klingenberg CP. 2013. Cranial integration and modularity: Insights into evolution and development from morphometric data. Hystrix-Italian Journal of Mammalogy 24(1):43-58.

Klingenberg CP, Badyaev AV, Sowry SM, Beckwith NJ. 2001. Inferring developmental modularity from morphological integration: Analysis of individual variation and asymmetry in bumblebee wings. American Naturalist 157(1):11-23.

Klingenberg CP, Mebus K, Auffray JC. 2003. Developmental integration in a complex morphological structure: How distinct are the modules in the mouse mandible? Evolution & Development 5(5):522-531.

Klug S. 2010. Monophyly, phylogeny and systematic position of the †Synechodontiformes (Chondrichthyes, Neoselachii). Zoologica Scripta 39(1):37-49.

Klug S, Kriwet J. 2010. Timing of deep-sea adaptation in dogfish sharks: Insights from a supertree of extinct and extant taxa. Zoologica Scripta 39(4):331-342.

Kocher TD. 2004. Adaptive evolution and explosive speciation: The cichlid fish model. Nature Reviews Genetics 5(4):288-298.

Kott E, Renaud CB, Vladykov VD. 1988. The urogenital papilla in the holarctic lamprey (Petromyzontidae). Environmental Biology of Fishes 23(1-2):37-43.

Kowalevsky AO. 1866. Entwickelungsgeschichte der einfachen Ascidien. Mémoires de l'Académie impériale des Sciences de St.-Pétersbourg : VII^{ème} Série 10(15):1-19.

Kuo C-H, Huang K-F, Mok H-K. 1994. Hagfishes of Taiwan (I): A taxonomic revision with description of four new *Paramyxine* species. Zoological Studies 33(2):126-139.

Kuratani S. 2009. Modularity, comparative embryology and evo-devo: Developmental dissection of evolving body plans. Developmental Biology 332(1):61-69.

Lacépède BGE. 1798. Histoire naturelle des poissons, Tome premier. Paris: Plassan. 532 p.

Lacépède BGE, Cuvier G, Desmarest MA-G. 1853. Histoire naturelle de Lacépède, Tome premier, comprenant les cétacées, les quadrupèdes ovipares, les serpents et les poissons. Bruxelles: Adolphe Deros et Comp. 654 p.

Lankester ER. 1870. Part I. - The Cephalaspidae. In: Powrie J, Lankester ER, editors. A Monograph of the Fishes of the Old Red Sandstone of Britain. London, UK: Palaeontographical Society. p 1-62.

Lankester ER. 1875. On some new points in the structure of *Amphioxus*, and their bearing on the morphology of Vertebrata. Quarterly Journal of Microscopical Science 15:257-267.

Lankester ER. 1889. Contributions to the knowledge of *Amphioxus lanceolatus*, Yarrell. Quarterly Journal of Microscopical Science 29(116):365-408.

Larouche O, Cloutier R, Zelditch ML. 2015. Head, body and fins: Patterns of morphological integration and modularity in fishes. Evolutionary Biology 42(3):296-311.

Larouche O, Zelditch ML, Cloutier R. 2017. Fin modules: An evolutionary perspective on appendage disparity in basal vertebrates. BMC Biology 15(1):1-26.

Lauder GV, Drucker EG. 2004. Morphology and experimental hydrodynamics of fish fin control surfaces. IEEE Journal of Oceanic Engineering 29(3):556-571.

Lauder GV, Liem KF. 1983. The evolution and interrelationships of the actinopterygian fishes. Bulletin of the Museum of Comparative Zoology 150(3):95-197.

Lauder GV, Nauen JC, Drucker EG. 2002. Experimental hydrodynamics and evolution: Function of median fins in ray-finned fishes. Integrative and Comparative Biology 42(5):1009-1017.

Lauritzen SL. 1996. Graphical Models. Oxford, UK: Clarendon Press. 298 p.

Lavoué S, Miya M, Arnegard ME, Sullivan JP, Hopkins CD, Nishida M. 2012. Comparable ages for the independent origins of electrogenesis in African and South American weakly electric fishes. PLoS One 7(5):18.

Lavoué S, Miya M, Inoue JG, Saitoh K, Ishiguro NB, Nishida M. 2005. Molecular systematics of the gonorynchiform fishes (Teleostei) based on whole mitogenome sequences: Implications for higher-level relationships within the Otocephala. Molecular Phylogenetics and Evolution 37(1):165-177.

Le HLV, Lecointre G, Perasso R. 1993. A 28S rRNA-based phylogeny of the gnathostomes: First steps in the analysis of conflict and congruence with morphologically based cladograms. Molecular Phylogenetics and Evolution 2(1):31-51.

Lehtola KA. 1983. Articulated Ordovician fish from Cañon City, Colorado. Journal of Paleontology 57(3):605-607.

Lemaire P. 2011. Evolutionary crossroads in developmental biology: The tunicates. Development 138(11):2143-2152.

Lewontin RC. 1974. The Genetic Basis of Evolutionary Change. New York, NY: Columbia University Press. 346 p.

Li B, Dettai A, Cruaud C, Couloux A, Desoutter-Meniger M, Lecointre G. 2009. RNF213, a new nuclear marker for acanthomorph phylogeny. Molecular Phylogenetics and Evolution 50(2):345-363.

Li CH, Matthes-Rosana KA, Garcia M, Naylor GJP. 2012. Phylogenetics of Chondrichthyes and the problem of rooting phylogenies with distant outgroups. Molecular Phylogenetics and Evolution 63(2):365-373.

Liem KF. 1973. Evolutionary strategies and morphological innovations: The cichlid pharyngeal jaws. Systematic Zoology 22(4):425-441.

Liem KF. 1980. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. American Zoologist 20(1):295-314.

Linde-Medina M, Boughner JC, Santana SE, Diogo R. 2016. Are more diverse parts of the mammalian skull more labile? Ecology and Evolution 6(8):2318-2324.

Lindsey CC. 1978. Form, function, and locomotory habits in fish. In: Hoar WS, Randall DJ, editors. Fish Physiology. Volume VII. Locomotion. New York, NY: Academic Press. p 1-100.

Liu Y. 1975. Lower Devonian agnathans of Yunnan and Sichuan. Vertebrata Palasiatica 13(10):202-216.

Long JA. 1995. The Rise of Fishes: 500 Million Years of Evolution. Baltimore: The John Hopkins University Press. 223 p.

Long JA, Clement AM. 2009. The postcranial anatomy of two Middle Devonian lungfishes (Osteichthyes, Dipnoi) from Mt. Howitt, Victoria, Australia. Memoirs of Museum Victoria 66(2):189-202.

Long JA, Mark-Kurik E, Johanson Z, Lee MSY, Young GC, Min Z, Ahlberg PE, Newman M, Jones R, den Blaauwen J and others. 2015. Copulation in antiarch placoderms and the origin of gnathostome internal fertilization. Nature 517(7533):196-199.

Long JA, Young GC, Holland T, Senden TJ, Fitzgerald EMG. 2006. An exceptional Devonian fish from Australia sheds light on tetrapod origins. Nature 444(7116):199-202.

López-Arbarello A. 2012. Phylogenetic interrelationships of ginglymodian fishes (Actinopterygii: Neopterygii). PLoS One 7(7).

López-Fernández H, Winemiller KO, Honeycutt RL. 2010. Multilocus phylogeny and rapid radiations in Neotropical cichlid fishes (Perciformes: Cichlidae: Cichlinae). Molecular Phylogenetics and Evolution 55(3):1070-1086.

Losos JB, Warheit KI, Schoener TW. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. Nature 387(6628):70-73.

Løvtrup S. 1977. The Phylogeny of Vertebrata. London, UK: John Wiley & Sons Ltd. 330 p.

Lowe CG, Moss GJ, Hoisington IV G, Vaudo JJ, Cartamil DP, Marcotte MM, Papastamatiou YP. 2007. Caudal spine shedding periodicity and site fidelity of round stingrays, *Urobatis halleri* (Cooper), at Seal Beach, California: Implications for stingray-related injury management. Bulletin of the Southern California Academy of Sciences 106(1):16-26.

Lu J, Giles S, Friedman M, den Blaauwen JL, Zhu M. 2016a. The oldest actinopterygian highlights the cryptic early history of the hyperdiverse ray-finned fishes. Current Biology 26:1-7.

Lu J, Zhu M. 2010. An onychodont fish (Osteichthyes, Sarcopterygii) from the Early Devonian of China, and the evolution of the Onychodontiformes. Proceedings of the Royal Society B-Biological Sciences 277(1679):293-299.

Lu J, Zhu M, Ahlberg PE, Qiao T, Zhu Y, Zhao W, Jia L. 2016b. A Devonian predatory fish provides insights into the early evolution of modern sarcopterygians. Science Advances 2(6):e1600154.

Lu J, Zhu M, Long JA, Zhao WJ, Senden TJ, Jia LT, Qiao T. 2012. The earliest known stem-tetrapod from the Lower Devonian of China. Nature Communications 3:7.

Lund R. 1985. Stethacanthid elasmobranch remains from the Bear Gulch Limestone (Namurian E2b) of Montana. American Museum Novitates(2828):1-24.

Lund R, Grogan ED. 1997. Relationships of the Chimaeriformes and the basal radiation of the Chondrichthyes. Reviews in Fish Biology and Fisheries 7(1):65-123.

Lund R, Grogan ED. 2004. Five new euchondrocephalan Chondrichthyes from the Bear Gulch Limestone (Serpukhovian, Namurian E2b) of Montana, USA. In: Arratia G, Wilson MVH, Cloutier R, editors. Recent Advances in the Origin and Early Radiation of Vertebrates. München, Germany: Verlag Dr. Friedrich Pfeil. p 505-531.

Lund R, Grogan ED, Fath M. 2014. On the relationships of the Petalodontiformes (Chondrichthyes). Paleontological Journal 48(9):1015-1029.

Luo HL, Hu SX, Chen LZ. 2001. New Early Cambrian chordates from Haikou, Kunming. Acta Geologica Sinica 75(4):345-348.

Mabee PM, Crotwell PL, Bird NC, Burke AC. 2002. Evolution of median fin modules in the axial skeleton of fishes. Journal of Experimental Zoology (Molecular and Developmental Evolution) 294(2):77-90.

Magwene PM. 2001. New tools for studying integration and modularity. Evolution 55(9):1734-1745.

Magwene PM. 2009. Statistical methods for studying modularity: A reply to Mitteroecker and Bookstein. Systematic Biology 58(1):146-149.

Mahler DL, Revell LJ, Glor RE, Losos JB. 2010. Ecological opportunity and the rate of morphological evolution in the diversification of greater antillean anoles. Evolution 64(9):2731-2745.

Maisey JG. 1984a. Chondrichthyan phylogeny: A look at the evidence. Journal of Vertebrate Paleontology 4(3):359-371.

Maisey JG. 1984b. Higher elasmobranch phylogeny and biostratigraphy. Zoological Journal of the Linnean Society 82(1-2):33-54.

Maisey JG. 1986. Heads and tails: A chordate phylogeny. Cladistics 2(3):201-256.

Maisey JG. 2009. The spine-brush complex in Symmoriiform sharks (Chondrichthyes; Symmoriiformes), with comments on dorsal fin modularity. Journal of Vertebrate Paleontology 29(1):14-24.

Maisey JG. 2012. What is an elasmobranch'? The impact of palaeontology in understanding elasmobranch phylogeny and evolution. Journal of Fish Biology 80(5):918-951.

Malashichev Y, Borkhvardt V, Christ B, Scaal M. 2005. Differential regulation of avian pelvic girdle development by the limb field ectoderm. Anatomy and Embryology 210(3):187-197.

Malashichev Y, Christ B, Prols F. 2008. Avian pelvis originates from lateral plate mesoderm and its development requires signals from both ectoderm and paraxial mesoderm. Cell and Tissue Research 331(3):595-604.

Mallatt J, Chen JY. 2003. Fossil sister group of craniates: Predicted and found. Journal of Morphology 258(1):1-31.

Mallatt J, Chen JY, Holland ND. 2003. Comment on "A new species of yunnanozoan with implications for deuterostome evolution". Science 300(5624).

Mallatt J, Holland N. 2013. *Pikaia gracilens* Walcott: Stem chordate, or already specialized in the Cambrian? Journal of Experimental Zoology Part B-Molecular and Developmental Evolution 320B(4):247-271.

Mallatt J, Sullivan J. 1998. 28S and 18S rDNA sequences support the monophyly of lampreys and hagfishes. Molecular Biology and Evolution 15(12):1706-1718.

Mallatt J, Sullivan J, Winchell CJ. 2001. The relationship of lampreys to hagfishes: a spectral analysis of ribosomal DNA sequences. In: Ahlberg PE, editor. Major Events in Early Vertebrate Evolution: Palaeontology, Phylogeny, Genetics and Development. London: Taylor & Francis. p 106-118.

Mantel N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Research 27(2):209-220.

Marchetti GM, Drton M, Sadeghi K. 2014. ggm: A package for graphical Markov models. Version 2.0.

Márquez EJ. 2008. A statistical framework for testing modularity in multidimensional data. Evolution 62(10):2688-2708.

Márquez EJ. 2014. Mint: Modularity and integration analysis tool for morphometric data. Version 1.61.

Marroig G, Cheverud JM. 2001. A comparison of phenotypic variation and covariation patterns and the role of phylogeny, ecology, and ontogeny during cranial evolution of New World monkeys. Evolution 55(12):2576-2600.

Marroig G, Shirai LT, Porto A, de Oliveira FB, De Conto V. 2009. The evolution of modularity in the mammalian skull II: Evolutionary consequences. Evolutionary Biology 36(1):136-148.

Märss T, Ritchie A. 1998. Articulated thelodonts (Agnatha) of Scotland. Transactions of the Royal Society of Edinburgh-Earth Sciences 88:143-195.

Märss T, Turner S, Karatajūtē-Talimaa V. 2007. Volume 1B - "Agnatha" II - Thelodonti. Schultze HP, editor. München, Germany: Verlag Dr. Friedrich Pfeil. 143 p.

McClure MM, McIntyre PB, McCune AR. 2006. Notes on the natural diet and habitat of eight danionin fishes, including the zebrafish *Danio rerio*. Journal of Fish Biology 69(2):553-570.

McCosker JE. 1977. The osteology, classification, and relationships of the eel family Ophichthidae. Proceedings of the California Academy of Science 41(1):1-123.

McCosker JE. 2004. A new species of finless snake eel (Anguilliformes: Ophichthidae) from Ascension island, with comments on *Ichthyapus acutirostris*. Proceedings of the California Academy of Science 55(7):169-173.

McCoy VE, Saupe EE, Lamsdell JC, Tarhan LG, McMahon S, Lidgard S, Mayer P, Whalen CD, Soriano C, Finney L and others. 2016. The 'Tully monster' is a vertebrate. Nature 532(7600):496-499.

McHenry MJ. 2005. The morphology, behavior, and biomechanics of swimming in ascidian larvae. Canadian Journal of Zoology 83(1):62-74.

McKinney ML, McNamara KJ. 1991. Heterochrony: The Evolution of Ontogeny. New York, NY: Plenum Press. 437 p.

McMillan CB, Wisner RL. 2004. Review of the hagfishes (Myxinidae, Myxiniformes) of the northwestern Pacific Ocean, with descriptions of three new species, *Eptatretus fernholmi*, *Paramyxine moki*, and *P. walkeri*. Zoological Studies 43(1):51-73.

McNeill Alexander R. 1967. Functional Design in Fishes. London, UK: Hutchinson & Co Ltd. 160 p.

Meek SE, Hildebrand SF. 1923. The marine fishes of Panama. Part I. Field Museum of Natural History Publication - Zoölogical Series 15(215):1-330.

Miles RS. 1970. Remarks on the vertebral column and caudal fin of acanthodian fishes. Lethaia 3(4):343-362.

Miles RS. 1973. Articulated acanthodian fishes from the Old Red Sandstone of England, with a review of the structure and evolution of the acanthodian shoulder-girdle. Bulletin of the British Museum (Natural History) - Geology 24(2):111-213.

Miles RS, Westoll TS. 1968. The placoderm fish *Coccosteus cuspidatus* Miller *ex* Agassiz from the Middle Old Red Sandstone of Scotland. Part 1. Descriptive morphology. Transactions of the Royal Society of Edinburgh 67(9):373-476.

Miller RF, Cloutier R, Turner S. 2003. The oldest articulated chondrichthyan from the Early Devonian period. Nature 425(6957):501-504.

Minelli A. 2016. Species diversity vs. morphological disparity in the light of evolutionary developmental biology. Annals of Botany 117(5):781-794.

Mivart SG. 1879. Notes on the fins of elasmobranchs, with considerations on the nature and homologues of vertebrate limbs. Transactions of the Zoological Society of London 10:439-484.

Miya M, Friedman M, Satoh TP, Takeshima H, Sado T, Iwasaki W, Yamanoue Y, Nakatani M, Mabuchi K, Inoue JG and others. 2013. Evolutionary origin of the Scombridae (tunas and mackerels): Members of a Paleogene adaptive radiation with 14 other pelagic fish families. PLoS One 8(9):1-19.

Miya M, Satoh TR, Nishida M. 2005. The phylogenetic position of toadfishes (order Batrachoidiformes) in the higher ray-finned fish as inferred from partitioned Bayesian analysis of 102 whole mitochondrial genome sequences. Biological Journal of the Linnean Society 85(3):289-306.

Miya M, Takeshima H, Endo H, Ishiguro NB, Inoue JG, Mukai T, Satoh TP, Yamaguchi M, Kawaguchi A, Mabuchi K and others. 2003. Major patterns of higher teleostean phylogenies: A new perspective based on 100 complete

mitochondrial DNA sequences. Molecular Phylogenetics and Evolution 26(1):121-138.

Miyashita T. 2012. Comparative analysis of the anatomy of the Myxinoidea and the ancestry of early vertebrate lineages. M.Sc. Thesis. Edmonton, Alberta: University of Alberta. 407 p.

Mok HK, Kuo CH. 2001. *Myxine formosana*, a new species of hagfish (Myxiniformes : Myxinidae) from the southwestern waters of Taiwan. Ichthyological Research 48(3):295-297.

Moloshnikov SV. 2008. Devonian antiarchs (Pisces, Antiarchi) from Central and Southern European Russia. Paleontological Journal 42(7):691-773.

Monteiro A. 2008. Alternative models for the evolution of eyespots and of serial homology on lepidopteran wings. Bioessays 30(4):358-366.

Monteiro LR, Bonato V, dos Reis SF. 2005. Evolutionary integration and morphological diversification in complex morphological structures: Mandible shape divergence in spiny rats (Rodentia, Echimyidae). Evolution & Development 7(5):429-439.

Morris SC. 1979. The Burgess Shale (Middle Cambrian) fauna. Annual Review of Ecology and Systematics 10:327-349.

Morris SC. 2006. Darwin's dilemma: The realities of the Cambrian 'explosion'. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 361(1470):1069-1083.

Morris SC. 2008. A redescription of a rare chordate, *Metaspriggina walcotti* Simonetta and Insom, from the Burgess Shale (Middle Cambrian), British Columbia, Canada. Journal of Paleontology 82(2):424-430.

Morris SC, Caron JB. 2012. *Pikaia gracilens* Walcott, a stem-group chordate from the Middle Cambrian of British Columbia. Biological Reviews 87:480-512.

Morris SC, Caron JB. 2014. A primitive fish from the Cambrian of North America. Nature 512(7515):419-U413.

Morris SC, Whittington HB. 1979. The animals of the Burgess Shale. Scientific American 241(1):122-133.

Moy-Thomas JA, Miles RS. 1971. Palaeozoic Fishes, Second edition. Philadelphia, PA: W. B. Saunders Company. 259 p.

Müller GB. 2007. Evo-devo: Extending the evolutionary synthesis. Nature Reviews Genetics 8(12):943-949.

Mulvany S, Motta PJ. 2013. The morphology of the cephalic lobes and anterior pectoral fins in six species of batoids. Journal of Morphology 274(9):1070-1083.

Murray AM, Wilson MVH. 2009. A new Late Cretaceous macrosemiid fish (Neopterygii, Halecostomi) from Morocco, with temporal and geographical range extensions for the family. Palaeontology 52:429-440.

Murray AM, Wilson MVH. 2014. Four new basal acanthomorph fishes from the Late Cretaceous of Morocco. Journal of Vertebrate Paleontology 34(1):34-48.

Naylor GJP, Caira JN, Jensen K, Rosana KAM, Straube N, Lakner C. 2012. Elasmobranch phylogeny: A mitochondrial estimate based on 595 species. In:

Carrier JC, Musick JA, Heithaus MR, editors. Biology of Sharks and their Relatives, Second Edition. Boca Raton, FL: CRC Press. p 31-56.

Naylor GJP, Ryburn JA, Fedrigo O, Lopez A. 2005. Phylogenetic relationships among the major lineages of modern elasmobranchs. In: Hamlett WC, editor. Reproductive Biology and Phylogeny of Chondrichthyes: Sharks, Batoids, and Chimaeras. Enfield, NH: Science Publishers. p 1-25.

Near TJ, Dornburg A, Eytan RI, Keck BP, Smith WL, Kuhn KL, Moore JA, Price SA, Burbrink FT, Friedman M and others. 2013. Phylogeny and tempo of diversification in the superradiation of spiny-rayed fishes. Proceedings of the National Academy of Sciences of the United States of America 110(31):12738-12743.

Near TJ, Eytan RI, Dornburg A, Kuhn KL, Moore JA, Davis MP, Wainwright PC, Friedman M, Smith WL. 2012. Resolution of ray-finned fish phylogeny and timing of diversification. Proceedings of the National Academy of Sciences of the United States of America 109(34):13698-13703.

Nelson JS. 2006. Fishes of the World. Fourth edition. Hoboken, NJ: John Wiley. 601 p.

Nelson JS, Grande TC, Wilson MVH. 2016. Fishes of the World. Fifth Edition. Hoboken, NJ: John Wiley & Sons, Inc. 707 p.

Nenadic O, Greenacre M. 2007. Correspondence analysis in R, with two- and three-dimensional graphics: The ca package. Journal of Statistical Software 20(3).

Newman MJ. 2002. A new naked jawless vertebrate from the Middle Devonian of Scotland. Palaeontology 45:933-941.

Newman MJ, Davidson RG, Den Blaauwen JL, Burrow CJ. 2012. The Early Devonian acanthodian *Uraniacanthus curtus* (Powrie, 1870) n. comb. from the Midland Valley of Scotland. Geodiversitas 34(4):739-759.

Newman MJ, Trewin NH. 2001. A new jawless vertebrate from the Middle Devonian of Scotland. Palaeontology 44:43-51.

Nishino A, Satoh N. 2001. The simple tail of chordates: Phylogenetic significance of appendicularians. Genesis 29(1):36-45.

Nixon KC. 1999. The Parsimony Ratchet, a new method for rapid parsimony analysis. Cladistics 15(4):407-414.

Novacek MJ. 2001. Mammalian phylogeny: Genes and supertrees. Current Biology 11(14):R573-R575.

Novitskaya LI, Turner S. 1998. *Turinia pagei* (Powrie): A new reconstruction of the soft organs of the cephalothorax. Memoirs of the Queensland Museum 42(2):533-544.

O'Meara BC, Ané C, Sanderson MJ, Wainwright PC. 2006. Testing for different rates of continuous trait evolution using likelihood. Evolution 60(5):922-933.

O'Toole B. 2002. Phylogeny of the species of the superfamily Echeneoidea (Perciformes: Carangoidei: Echeneidae, Rachycentridae, and Coryphaenidae), with an interpretation of echeneid hitchhiking behaviour. Canadian Journal of Zoology 80(4):596-623.

Ogburn RM, Edwards EJ. 2009. Anatomical variation in Cactaceae and relatives: Trait lability and evolutionary innovation. American Journal of Botany 96(2):391-408.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H. 2013. vegan: Community ecology package. Version 2.0-10.

Olson EC, Miller RL. 1958. Morphological Integration. Chicago, IL: The University of Chicago Press. 317 p.

Ørvig T. 1967. Some new acanthodian material from the Lower Devonian of Europe. Journal of the Linnean Society of London, Zoology 47(311):131-153.

Osburn RC. 1907. Observations on the origin of the paired limbs of vertebrates. American Journal of Anatomy 7(2):171-194.

Otero O. 1997. A new genus *Aipichthyoidea* (Teleostei, Acanthomorpha) from the Lower Cenomanian of Hgula (Lebanon): Description and phylogenetic relationships. Comptes Rendus de l'Académie des Sciences Série II Fascicule a - Sciences de la Terre et des Planètes 325(6):453-458.

Otero O, Gayet M. 1996. Anatomy and phylogeny of the Aipichthyoydea nov. of the Cenomanian Tethys and their place in the Acanthomorpha (Teleostei). Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen 202(3):313-344.

Owen R. 1846. Lectures on the comparative anatomy and physiology of the vertebrate animals, delivered at the Royal College of Surgeons of England in 1844 and 1846, Part I - Fishes. London: Longman, Brown, Green and Longmans. 308 p.

Owen R. 1849. On the nature of limbs, a discourse delivered on Friday, February 9, at an evening meeting of the Royal Institution of Great Britain. London: John Van Voorst, Paternoster Row. 119 p.

Owen R. 1854. The Principal Forms of the Skeleton and of the Teeth. Philadelphia: Blanchard and Lea. 329 p.

Pan J. 1992. New Galeaspids (Agnatha) from the Silurian and Devonian of China. Beijing, China: Geological Publishing House. 86 p.

Parsons KJ, Márquez EJ, Albertson RC. 2012. Constraint and opportunity: The genetic basis and evolution of modularity in the cichlid mandible. American Naturalist 179(1):64-78.

Patten W. 1904. New fact concerning *Bothriolepis*. Biological Bulletin 7(2):113-124.

Patterson C. 1982. Morphological characters and homology. In: Joysey KA, Friday AE, editors. Problems of Phylogenetic Reconstruction. London, UK: Academic Press. p 21-74.

Patterson C. 1988. Homology in classical and molecular biology. Molecular Biology and Evolution 5(6):603-625.

Pavan-Kumar A, Gireesh-Babu P, Babu PPS, Jaiswar AK, Krishna V, Prasasd KP, Chaudhari A, Raje SG, Chakraborty SK, Krishna G and others. 2014. Molecular phylogeny of elasmobranchs inferred from mitochondrial and nuclear markers. Molecular Biology Reports 41(1):447-457.

Pavlicev M, Hansen TF. 2011. Genotype-phenotype maps maximizing evolvability: Modularity revisited. Evolutionary Biology 38(4):371-389.

Philippe H, Lartillot N, Brinkmann H. 2005. Multigene analyses of bilaterian animals corroborate the monophyly of Ecdysozoa, Lophotrochozoa, and Protostomia. Molecular Biology and Evolution 22(5):1246-1253.

Phillips GL. 1969. Morphology and variation of the American cyprinid fishes *Chrosomus erythrogaster* and *Chrosomus eos*. Copeia 1969(3):501-509.

Pietsch TW. 1984. Lophiiformes: Development and relationships. In: Moser HG, Richards WJ, Cohen DM, Fahay MP, Kendall AW, Richardson SL, editors. Ontogeny and Systematics of Fishes. Based on an international symposium dedicated to the memory of Elbert Halvor Ahlstrom. Lawrence, KS: The American Society of Ichthyologists and Herpetologists. p 320-325.

Pietsch TW, Orr JW. 2007. Phylogenetic relationships of deep-sea anglerfishes of the suborder Ceratioidei (Teleostei : Lophiiformes) based on morphology. Copeia 2007(1):1-34.

Plaut I, Gordon MS. 1994. Swimming metabolism of wild-type and cloned zebrafish *Brachydanio rerio*. Journal of Experimental Biology 194(1):209-223.

Pletcher FT. 1963. The life history and distribution of lampreys in the Salmon and certain other rivers in British Columbia, Canada. M.Sc. Thesis. Vancouver, BC: University of British Columbia. 195 p.

Poplin C, Sotty D, Janvier P. 2001. Un myxinoïde (Craniata, Hyperotreti) dans le *Konservat-Lagerstätte* Carbonifère supérieur de Montceau-les-Mines (Allier, France). Comptes Rendus de l'Académie des Sciences Série II Fascicule a - Sciences de la Terre et des Planètes 332:345-350.

Porto A, de Oliveira FB, Shirai LT, De Conto V, Marroig G. 2009. The evolution of modularity in the mammalian skull I: Morphological integration patterns and magnitudes. Evolutionary Biology 36(1):118-135.

Poss SG, Boschung HT. 1996. Lancelets (Cephalochordata: Branchiostomatidae): How many species are valid? Israel Journal of Zoology 42(Suppl.):13-66.

Powrie J. 1870. On the earliest known vestiges of vertebrate life; being a description of the fish remains of the Old Red Sandstone rocks of Forfarshire. Transactions of the Edinburgh Geological Society 1(3):284-301.

Pradel A, Sansom IJ, Gagnier P-Y, Cespedes R, Janvier P. 2007. The tail of the Ordovician fish *Sacabambaspis*. Biology Letters 3(1):72-75.

Pridmore PA, Barwick RE, Nicoll RS. 1997. Soft anatomy and the affinities of conodonts. Lethaia 29(4):317-328.

Purnell MA. 1995. Microwear on conodont elements and macrophagy in the first vertebrates. Nature 374(6525):798-800.

Purvis A. 1995a. A composite estimate of primate phylogeny. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 348(1326):405-421.

Purvis A. 1995b. A modification to Baum and Ragan's method for combining phylogenetic trees. Systematic Biology 44(2):251-255.

Putnam NH, Butts T, Ferrier DEK, Furlong RF, Hellsten U, Kawashima T, Robinson-Rechavi M, Shoguchi E, Terry A, Yu JK and others. 2008. The amphioxus genome and the evolution of the chordate karyotype. Nature 453(7198):1064-U3.

Qiao T, King B, Long JA, Ahlberg P, Zhu M. 2016. Early gnathostome phylogeny revisited: Multiple method consensus. PLoS One 11(9):e0163157.

R Core Team. 2014. R: A language and environment for statistical computing. Version 3.0.3. Vienna, Austria: R Foundation for Statistical Computing

R Core Team. 2016. R: A language and environment for statistical computing. Version 3.2.4. Vienna, Austria: R Foundation for Statistical Computing.

Rade CM, Ward AB. 2010. Evolution of fin size and morphology in otophysan fishes. Integrative and Comparative Biology 50:E285.

Raff RA. 1996. The Shape of Life: Genes, Development, and the Evolution of Animal Form. Chicago, IL: The University of Chicago Press. 544 p.

Ragan MA. 1992. Phylogenetic inference based on matrix representation of trees. Molecular Phylogenetics and Evolution 1(1):53-58.

Reif W-E. 2006. Conodonts, odontodes, stem-groups, and the ancestry of enamel genes. Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen 241(3):405-439.

Reif WE. 1982. Evolution of dermal skeleton and dentition in vertebrates: The odontode regulation theory. In: Hecht MK, Wallace B, Prance GT, editors. Evolutionary Biology. New York, NY: Plenum Press. p 287-368.

Reimchen TE, Temple NF. 2004. Hydrodynamic and phylogenetic aspects of the adipose fin in fishes. Canadian Journal of Zoology 82(6):910-916.

Renaud CB. 2011. Lampreys of the world. An annotated and illustrated catalogue of lamprey species known to date. In: FAO, editor. FAO species catalogue for fishery purposes. Rome: FAO.

Revell LJ, Harmon LJ, Collar DC. 2008. Phylogenetic signal, evolutionary process, and rate. Systematic Biology 57(4):591-601.

Rice HJ. 1880. Observations upon the habits, structure and development of *Amphioxus lanceolatus*. American Naturalist 14(1):1-19.

Richardson ES. 1966. Wormlike fossil from the Pennsylvanian of Illinois. Science 151(3706):75-76.

Richardson LR. 1953. *Neomyxine* n.g. (Cyclostomata) based on *Myxine biniplicata* Richardson and Jowett 1951, and further data on the species. Transactions of the Royal Society of New Zealand 81:379-383.

Richardson LR. 1958. A new genus and species of Myxinidae. Transactions of the Royal Society of New Zealand 85:283-287.

Richtsmeier JT, Lele SR, Cole III TM. 2005. Landmark morphometrics and the analysis of variation. In: Hallgrímsson B, Hall BK, editors. Variation: A Central Concept in Biology. Amsterdam, Netherlands: Elsevier Academic Press. p 49-69.

Riedl R. 1978. Order in Living Organisms: A Systems Analysis of Evolution. Jefferies RPS, translator. Chichester, UK: John Wiley & Sons. 313 p.

Riley C, Cloutier R, Grogan ED. 2017. Similarity of morphological composition and developmental patterning in paired fins of the elephant shark. Scientific Reports 7(9985):1-10.

Ritchie A. 1964. New light on the morphology of the Norwegian Anaspida. Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo. I. Matematiske-naturvidenskapslige Klasse, Ny Serie 14:1-35.

Ritchie A. 1967. *Ateleaspis tesselata* Traquair, a non-cornuate cephalaspid from the Upper Silurian of Scotland. Journal of the Linnean Society of London, Zoology 47(311):69-81.

Ritchie A. 1968a. New evidence on *Jamoytius kerwoodi* White, an important ostracoderm from the Silurian of Lanarkshire, Scotland. Palaeontology 11(1):21-39.

Ritchie A. 1968b. *Phlebolepis elegans* Pander, an Upper Silurian thelodont from Oesel, with remarks on the morphology of thelodonts. In: Ørvig T, editor. Current Problems of Lower Vertebrate Phylogeny: Proceeding of the Fourth Nobel Symposium. Stockholm, Sweden: Almqvist & Wiskell. p 81-88.

Ritchie A. 1980. The Late Silurian anaspid genus *Rhyncholepis* from Oesel, Estonia, and Ringerike, Norway. American Museum Novitates 2699:1-18.

Ritchie A. 1985. *Arandaspis prionotolepis*, the southern four-eyed fish. In: Rich PV, Van Tets GF, Knight F, editors. Kadimakara: Extinct Vertebrates from Australia. Victoria, Australia: Pioneer Design Studio. p 95-101.

Ritchie A, Gilbert-Tomlinson J. 1977. First Ordovician vertebrates from the southern hemisphere. Alcheringa 1(4):351-368.

Roberts TR. 1981. Sundasalangidae, a new family of minute freshwater salmoniform fishes from southeast Asia. Proceedings of the California Academy of Sciences 42(9):295-302.

Robertson GM. 1935a. *Oeselaspis*, a new genus of ostracoderm. American Journal of Science 5(29):453-461.

Robertson GM. 1935b. The ostracoderm genus *Dartmuthia* Patten. American Journal of Science(29):323-335.

Robertson GM. 1938a. The Tremataspidae. Part I. American Journal of Science 35(207):172-206.

Robertson GM. 1938b. The Tremataspidae. Part II. American Journal of Science 35(208):273-296.

Robertson GM. 1941. The ostracoderm order Anaspida, with description of some Upper Silurian material. Transactions of the Kansas Academy of Science 44:314-317.

Rodrigo AG. 1993. A comment on Baum's method for combining phylogenetic trees. Taxon 42(3):631-636.

Rodrigo AG. 1996. On combining cladograms. Taxon 45(2):267-274.

Rohlf FJ. 2013a. tps Utiliy Program. Version 1.58. Stony Brook University, NY.

Rohlf FJ. 2013b. tpsDig. Version 2.17. Stony Brook University, NY.
Rohlf FJ, Slice D. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. Systematic Zoology 39(1):40-59.
Rondelet G. 1558. La première partie de l'histoire entière des poissons. Lyon: La Masse d'Or. 418 p.
Rosen DE. 1982. Teleostean interrelationships, morphological function and evolutionary inference. American Zoologist 22(2):261-273.
Rosenberger LJ. 2001. Pectoral fin locomotion in batoid fishes: Undulation versus oscillation. Journal of Experimental Biology 204(2):379-394.
Rowe T. 2004. Chordate phylogeny and development. In: Cracraft J, Donoghue MJ, editors. Assembling the Tree of Life. New York, NY: Oxford University Press. p 384-409.
Ruvinsky I, Gibson-Brown JJ. 2000. Genetic and developmental bases of serial homology in vertebrate limb evolution. Development 127(24):5233-5244.
Saitoh K, Miya M, Inoue JG, Ishiguro NB, Nishida M. 2003. Mitochondrial genomics of ostariophysan fishes: Perspectives on phylogeny and biogeography. Journal of Molecular Evolution 56(4):464-472.
Salzburger W, Meyer A, Baric S, Verheyen E, Sturmbauer C. 2002. Phylogeny of the Lake Tanganyika cichlid species flock and its relationship to the Central and East African haplochromine cichlid fish faunas. Systematic Biology 51(1):113-135.
Sampson PD, Bookstein FL, Sheehan H, Bolson EL. 1996. Eigenshape analysis of left ventricular outlines from contrast ventriculograms. In: Marcus LF, Corti M, Loy A, Naylor GJP, Slice DE, editors. Advances in Morphometrics. New York: Plenum Press. p 131-152.
Sánchez-Villagra MR, Goswami A, Weisbecker V, Mock O, Kuratani S. 2008. Conserved relative timing of cranial ossification patterns in early mammalian evolution. Evolution & Development 10(5):519-530.
Sandon H. 1956. An abnormal specimen of *Synodontis membranaceus* (Teleostei, Siluroidea), with a discussion on the evolutionary history of the adipose fin in fish. Proceedings of the Zoological Society of London 127(4):453-459.
Sanger TJ, Mahler DL, Abzhanov A, Losos JB. 2012. Roles for modularity and constraint in the evolution of cranial diversity among *Anolis* lizards. Evolution 66(5):1525-1542.
Sansom IJ, Donoghue PCJ, Albanesi G. 2005. Histology and affinity of the earliest armoured vertebrate. Biology Letters 1(4):446-449.
Sansom IJ, Smith MM, Smith MP. 1996. Scales of thelodont and shark-like fishes from the Ordovician of Colorado. Nature 379(6566):628-630.
Sansom IJ, Smith MP, Armstrong HA, Smith MM. 1992. Presence of the earliest vertebrate hard tissues in conodonts. Science 256(5061):1308-1311.
Sansom IJ, Smith MP, Smith MM. 1994. Dentine in conodonts. Nature 368(6472):591.
Sansom IJ, Smith MP, Smith MM, Turner P. 1997. *Astraspis* - The anatomy and histology of an Ordovician fish. Palaeontology 40:625-643.

Sansom R. 2007. A review of the problematic osteostracan genus *Auchenaspis* and its role in Thyestidian evolution. Palaeontology 50:1001-1011.

Sansom RS. 2008. The origin and early evolution of the Osteostraci (Vertebrata): A phylogeny for the Thyestiida. Journal of Systematic Palaeontology 6(3):317-332.

Sansom RS. 2009. Phylogeny, classification and character polarity of the Osteostraci (Vertebrata). Journal of Systematic Palaeontology 7(1):95-115.

Sansom RS, Freedman K, Gabbott SE, Aldridge RJ, Purnell MA. 2010. Taphonomy and affinity of an enigmatic Silurian vertebrate, *Jamoytius kerwoodi* White. Palaeontology 53:1393-1409.

Sansom RS, Gabbott SE, Purnell MA. 2013. Unusual anal fin in a Devonian jawless vertebrate reveals complex origins of paired appendages. Biology Letters 9(3):5.

Satoh N, Rokhsar D, Nishikawa T. 2014. Chordate evolution and the three-phylum system. Proceedings of the Royal Society B-Biological Sciences 281(1794):10.

Savriama Y, Vitulo M, Gerber S, Debat V, Fusco G. 2016. Modularity and developmental stability in segmented animals: variation in translational asymmetry in geophilomorph centipedes. Development Genes and Evolution Published online:1-10.

Schaefer JT, Summers AP. 2005. Batoid wing skeletal structure: Novel morphologies, mechanical implications, and phylogenetic patterns. Journal of Morphology 264(3):298-313.

Schaeffer B. 1981. The xenacanth shark neurocranium, with comments on elasmobranch monophyly. Bulletin of the American Museum of Natural History 169:1-66.

Schaeffer B. 1987. Deuterostome monophyly and phylogeny. Evolutionary Biology 21:179-235.

Schaeffer B, Thomson KS. 1980. Reflections on agnathan-gnathostome relationships. In: Jacobs LL, editor. Aspects of Vertebrate History. Flagstaff, Arizona: Museum of Northern Arizona Press. p 19-33.

Schaeffer B, Williams M. 1977. Relationships of fossil and living elasmobranchs. American Zoologist 17(2):293-302.

Scheiner SM. 1993. Genetics and evolution of phenotypic plasticity. Annual Review of Ecology and Systematics 24:35-68.

Schlager S. 2016. Morpho: Calculations and visualisations related to geometric morphometrics. Version 2.4.

Schliep KP. 2011. phangorn: Phylogenetic analysis in R. Bioinformatics 27(4):592-593.

Schlosser G, Wagner GP. 2004. Introduction: The modularity concept in developmental and evolutionary biology. In: Schlosser G, Wagner GP, editors. Modularity in Development and Evolution. Chicago, IL: The University of Chicago Press. p 1-11.

Schluter D. 1996. Ecological causes of adaptive radiation. American Naturalist 148:S40-S64.

Schmalhausen JJ. 1913. Zur Morphologie der unpaaren Flossen. II. Bau und Phylogenese der unpaaren Flossen und insbesonders der Schwanzflosse der Fische Zeitschrift für wissenschaftliche Zoologie 104:1-80.

Schubert M, Escriva H, Xavier-Neto J, Laudet V. 2006. Amphioxus and tunicates as evolutionary model systems. Trends in Ecology & Evolution 21(5):269-277.

Schubert M, Holland LZ, Holland ND. 2000. Characterization of an amphioxus *Wnt* gene, *AmphiWnt11*, with possible roles in myogenesis and tail outgrowth. Genesis 27(1):1-5.

Schultze H-P. 1986. Dipnoans as sarcopterygians. Journal of Morphology 190(Supplement S1):39-74.

Schultze H-P. 1993. Osteichthyes: Sarcopterygii. In: Benton MJ, editor. The Fossil Record 2. London, UK: Chapman & Hall. p 657-663.

Schultze H-P. 1996. Conodont histology: An indicator of vertebrate relationship? Modern Geology 20(3-4):275-285.

Schultze H-P, Cumbaa SL. 2001. *Dialipina* and the characters of basal actinopterygians. In: Ahlberg PE, editor. Major Events in Early Vertebrate Evolution: Palaeontology, Phylogeny, Genetics and Development. London: Taylor & Francis. p 315-332.

Scott BR, Wilson MVH. 2012. A new species of *Waengsjoeaspis* (Cephalaspidomorpha, Osteostraci) from the Early Devonian of northwestern Canada, with a redescription of *W. nahanniensis* and implications for growth, variation, morphology, and phylogeny. Journal of Vertebrate Paleontology 32(6):1235-1253.

Scott BR, Wilson MVH. 2013. A new species of osteostracan from the Lochkovian (Early Devonian) of the Mackenzie Mountains, with comments on body size, growth, and geographic distribution in the genus *Machairaspis*. Canadian Journal of Earth Sciences 50(2):127-134.

Scott WB, Crossman EJ. 1973. Freshwater fishes of Canada. Bulletin of the Fisheries Research Board of Canada 184:1-966.

Sears KE. 2014. Differences in growth generate the diverse palate shapes of new world leaf-nosed bats (Order Chiroptera, Family Phyllostomidae). Evolutionary Biology 41(1):12-21.

Sears KE, Bianchi C, Powers L, Beck AL. 2013. Integration of the mammalian shoulder girdle within populations and over evolutionary time. Journal of Evolutionary Biology 26(7):1536-1548.

Sequeira SEK, Coates MI. 2000. Reassessment of '*Cladodus*' *neilsoni* Traquair: A primitive shark from the Lower Carboniferous of East Kilbride, Scotland. Palaeontology 43:153-172.

Setiamarga DHE, Miya M, Yamanoue Y, Mabuchi K, Satoh TP, Inoue JG, Nishida M. 2008. Interrelationships of Atherinomorpha (medakas, flyingfishes, killifishes,

silversides, and their relatives): The first evidence based on whole mitogenome sequences. Molecular Phylogenetics and Evolution 49(2):598-605.
Sfakiotakis M, Lane DM, Davies JBC. 1999. Review of fish swimming modes for aquatic locomotion. IEEE Journal of Oceanic Engineering 24(2):237-252.
Shenkar N, Swalla BJ. 2011. Global diversity of Ascidiacea. PLoS One 6(6):12.
Shimeld SM, Donoghue PCJ. 2012. Evolutionary crossroads in developmental biology: Cyclostomes (lamprey and hagfish). Development 139(12):2091-2099.
Shimeld SM, Holland PWH. 2000. Vertebrate innovations. Proceedings of the National Academy of Sciences of the United States of America 97(9):4449-4452.
Shirai S. 1992. Phylogenetic relationships of the angel sharks, with comments on elasmobranch phylogeny (Chondrichthyes, Squatinidae). Copeia 1992(2):505-518.
Shirai S. 1996. Phylogenetic interrelationships of neoselachians (Chondrichthyes, Euselachii). In: Stiassny MLJ, Parenti LR, Johnson GD, editors. Interrelationships of Fishes. San Diego, CA: Academic Press. p 9-34.
Shu D-G, Morris SC, Zhang X-L. 1996a. A *Pikaia*-like chordate from the Lower Cambrian of China. Nature 384(6605):157-158.
Shu D. 2008. Cambrian explosion: Birth of tree of animals. Gondwana Research 14(1-2):219-240.
Shu D, Chen L, Zhang X-L, Han J, Li Y. 2001. Chengjiang Lagerstätte and earliest-known chordates. Zoological Science 18(4):447-448.
Shu D, Zhang X, Chen L. 1996b. Reinterpretation of *Yunnanozoon* as the earliest known hemichordate. Nature 380(6573):428-430.
Shu DG. 2003. A paleontological perspective of vertebrate origin. Chinese Science Bulletin 48(8):725-735.
Shu DG. 2005. On the phylum Vetulicolia. Chinese Science Bulletin 50(20):2342-2354.
Shu DG, Luo HL, Morris SC, Zhang XL, Hu SX, Chen L, Han J, Zhu M, Li Y, Chen LZ. 1999. Lower Cambrian vertebrates from South China. Nature 402(6757):42-46.
Shu DG, Morris SC. 2003. Response to comment on "A new species of yunnanozoan with implications for deuterostome evolution". Science 300(5624).
Shu DG, Morris SC, Han J, Zhang ZF, Yasui K, Janvier P, Chen L, Zhang XL, Liu JN, Li Y and others. 2003a. Head and backbone of the Early Cambrian vertebrate *Haikouichthys*. Nature 421(6922):526-529.
Shu DG, Morris SC, Zhang ZF, Han J. 2010. The earliest history of the deuterostomes: The importance of the Chengjiang Fossil-Lagerstatte. Proceedings of the Royal Society B-Biological Sciences 277(1679):165-174.
Shu DG, Morris SC, Zhang ZF, Liu JN, Han J, Chen L, Zhang XL, Yasui K, Li Y. 2003b. A new species of yunnanozoan with implications for deuterostome evolution. Science 299(5611):1380-1384.
Shubin N, Tabin C, Carroll S. 1997. Fossils, genes and the evolution of animal limbs. Nature 388(6643):639-648.

Shubin N, Tabin C, Carroll S. 2009. Deep homology and the origins of evolutionary novelty. Nature 457(7231):818-823.

Shubin NH. 2002. Origin of evolutionary novelty: Examples from limbs. Journal of Morphology 252(1):15-28.

Shubin NH, Daeschler EB, Jenkins FA. 2006. The pectoral fin of *Tiktaalik roseae* and the origin of the tetrapod limb. Nature 440(7085):764-771.

Shubin NH, Daeschler EB, Jenkins FA. 2014. Pelvic girdle and fin of *Tiktaalik roseae*. Proceedings of the National Academy of Sciences of the United States of America 111(3):893-899.

Shubin NH, Davis MC. 2004. Modularity in the evolution of vertebrate appendages. In: Schlosser G, Wagner GP, editors. Modularity in Development and Evolution. Chicago, IL: The University of Chicago Press. p 429-440.

Sidlauskas B. 2007. Testing for unequal rates of morphological diversification in the absence of a detailed phylogeny: A case study from characiform fishes. Evolution 61(2):299-316.

Sidlauskas B. 2008. Continuous and arrested morphological diversification in sister clades of characiform fishes: A phylomorphospace approach. Evolution 62(12):3135-3156.

Siebert DJ. 1997. Notes on the anatomy and relationships of *Sundasalanx* Roberts (Teleostei, Clupeidae), with descriptions of four new species from Borneo. Bulletin of the Natural History Museum, London. Zoology Series 63(1):13-26.

Simon HA. 1962. The architecture of complexity. Proceedings of the American Philosophical Society 106(6):467-482.

Simonetta AM, Insom E. 1993. New animals from the Burgess Shale (Middle Cambrian) and their possible significance for the understanding of the Bilateria. Bollettino di Zoologia 60(1):97-107.

Singh TR, Tsagkogeorga G, Delsuc F, Blanquart S, Shenkar N, Loya Y, Douzery EJP, Huchon D. 2009. Tunicate mitogenomics and phylogenetics: peculiarities of the *Herdmania momus* mitochondrial genome and support for the new chordate phylogeny. BMC Genomics 10(1):534.

Smith HM. 1907. The Fishes of North Carolina. Pratt JH, editor. Raleigh, NC: North Carolina Geological and Economic Survey. 453 p.

Smith MM, Sansom IJ, Smith MP. 1996. 'Teeth' before armour: The earliest vertebrate mineralized tissues. Modern Geology 20(3-4):303-319.

Smith MP, Sansom IJ, Cochrane KD. 2001. The Cambrian origin of vertebrates. In: Ahlberg PE, editor. Major Events in Early Vertebrate Evolution: Palaeontology, Phylogeny, Genetics and Development. London: Taylor & Francis. p 67-84.

Snitting D. 2008. A redescription of the anatomy of the Late Devonian *Spodichthys buetleri* Jarvik, 1985 (Sarcopterygii, Tetrapodomorpha) from East Greenland. Journal of Vertebrate Paleontology 28(3):637-655.

Soehn KL, Wilson MVH. 1990. A complete, articulated heterostracan from Wenlockian (Silurian) beds of the Delorme group, Mackenzie Mountains,

Northwest Territories, Canada. Journal of Vertebrate Paleontology 10(4):405-419.
Springer MS, de Jong WW. 2001. Phylogenetics - Which mammalian supertree to bark up? Science 291(5509):1709-1711.
Springer VG, Orrell TM. 2004. Phylogenetic analysis of the families of acanthomorph fishes based on dorsal gill-arch muscles and skeleton. Bulletin of the Biological Society of Washington Number 11:237-260.
Stahl BJ. 1999. Volume 4 - Chondrichthyes III - Holocephali. Schultze H-P, editor. München, Germany: Verlag Dr. Friedrich Pfeil.
Standen EM. 2008. Pelvic fin locomotor function in fishes: Three-dimensional kinematics in rainbow trout (*Oncorhynchus mykiss*). Journal of Experimental Biology 211(18):2931-2942.
Stensiö EA. 1927. The Downtonian and Devonian vertebrates of Spitsbergen. Part I. Family Cephalaspidae. Skrifter om Svalbard og Nordishavet(12):1-391.
Stensiö EA. 1932. The Cephalaspids of Great Britain. London, UK: British Miseum (Natural History). 220 p.
Stensiö EA. 1939. A new anaspid from the Upper Devonian of Scaumenac Bay in Canada, with remarks on the other anaspids. Kungliga Svenska Vetenskapsakademiens Handlingar 18(1):1-25.
Stensiö EA. 1948. On the Placodermi of the Upper Devonian of East Greenland. II. Antiarchi: Subfamily Bothriolepinae. With an attempt at a revision of the previously described species of that family. Meddelelser om Grønland 139:1-622.
Stensiö EA. 1964. Les cyclostomes fossiles ou ostracodermes. In: Piveteau J, editor. Traité de Paléontologie. Tome IV. L'origine des vertébrés, leur expansion dans les eaux douces et le milieu marin. Premier Volume: Vertébrés (généralités), agnathes. Paris, France: Masson et Cie. p 96-382.
Stetson HC. 1928. A restoration of the anaspid *Birkenia elegans* Traquair. Journal of Geology 36(5):458-470.
Stewart TA. 2015. The origin of a new fin skeleton through tinkering. Biology Letters 11(7):5.
Stewart TA, Hale ME. 2013. First description of a musculoskeletal linkage in an adipose fin: Innovations for active control in a primitively passive appendage. Proceedings of the Royal Society B-Biological Sciences 280(1750):20122159.
Stewart TA, Smith WL, Coates MI. 2014. The origins of adipose fins: An analysis of homoplasy and the serial homology of vertebrate appendages. Proceedings of the Royal Society B-Biological Sciences 281(1781):20133120.
Stock DW, Whitt GS. 1992. Evidence from 18S ribosomal RNA sequences that lampreys and hagfishes form a natural group. Science 257(5071):787-789.
Stokes MD. 1996. Larval settlement, post-settlement growth and secondary production of the Florida lancelet (= amphioxus) *Branchiostoma floridae*. Marine Ecology Progress Series 130(1-3):71-84.
Stokes MD, Holland ND. 1998. The lancelet. American Scientist 86(6):552-560.

Storms R. 1888. The adhesive disk of *Echeneis*. The Annals and Magazine of Natural History, Sixth Series 2(7):67-76.

Swartz B. 2012. A marine stem-tetrapod from the Devonian of western North America. PLoS One 7(3):11.

Sweet WC. 1988. The Conodonta: Morphology, Taxonomy, Paleoecology, and Evolutionary History od a Long-Extinct Animal Phylum. Oxford, UK: Clarendon Press. 212 p.

Sweet WC, Donoghue PCJ. 2001. Conodonts: Past, present, future. Journal of Paleontology 75(6):1174-1184.

Tabin C, Laufer E. 1993. *Hox* genes and serial homology. Nature 361(6414):692-693.

Takahashi T. 2003. Systematics of Tanganyikan cichlid fishes (Teleostei : Perciformes). Ichthyological Research 50(4):367-382.

Tamura K, Kuraishi R, Saito D, Masaki H, Ide H, Yonei-Tamura S. 2001. Evolutionary aspects of positioning and identification of vertebrate limbs. Journal of Anatomy 199:195-204.

Tanaka M. 2013. Molecular and evolutionary basis of limb field specification and limb initiation. Development Growth & Differentiation 55(1):149-163.

Tanaka M, Cohn MJ, Ashby P, Davey M, Martin P, Tickle C. 2000. Distribution of polarizing activity and potential for limb formation in mouse and chick embryos and possible relationships to polydactyly. Development 127(18):4011-4021.

Tanaka M, Munsterberg A, Anderson WG, Prescott AR, Hazon N, Tickle C. 2002. Fin development in a cartilaginous fish and the origin of vertebrate limbs. Nature 416(6880):527-531.

Tanaka M, Onimaru K. 2012. Acquisition of the paired fins: A view from the sequential evolution of the lateral plate mesoderm. Evolution & Development 14(5):412-420.

Tarlo LB. 1964. Psammosteiformes (Agnatha) - A review with descriptions of new material from the Lower Devonian of Poland. I. General part. Paleontologia Polonica(13):1-135.

Tarlo LB. 1965. Psammosteiformes (Agnatha) - A review with descriptions of new material from the Lower Devonian of Poland. II. Systematic part. Paleontologia Polonica(15):1-167.

Taverne L. 1997. *Osorioichthys marginis*, "Paléonisciforme" du Famennien de Belgique, et la phylogénie des actinoptérygiens dévoniens (Pisces). Bulletin de l'Institut royal des Sciences naturelles de Belgique 67:57-78.

Temple NF, Reimchen TE. 2008. Adipose fin condition and flow regime in catfish. Canadian Journal of Zoology 86(9):1079-1082.

Thacher JK. 1877. Median and paired fins, a contribution to the history of vertebrate limbs. Transactions of the Connecticut Academy of Arts and Science 3:281-308.

Thomas G, Freckleton RP. 2012. motmot: Models of trait macroevolution on trees. Version 1.1.2.

Thorson TB, Langhammer JK, Oetinger MI. 1988. Periodic shedding and replacement of venomous caudal spines, with special reference to South American freshwater stingrays, *Potamotrygon* spp. Environmental Biology of Fishes 23(4):299-314.

Tinker SW. 1944. Hawaiian Fishes. A Hanbook of the Fishes Found Among the Islands of the Central Pacific Ocean. Honolulu, Hawaii: Tongg Publishing Company. 404 p.

Traquair RH. 1900. Report on fossil fishes collected by the geological survey of Scotland in the Silurian rocks of the south of Scotland. Transactions of the Royal Society of Edinburgh 39(3):827-864.

Trinajstic K, Boisvert C, Long J, Maksimenko A, Johanson Z. 2014. Pelvic and reproductive structures in placoderms (stem gnathostomes). Biological Reviews 90(2):467-501.

Tulenko FJ, McCauley DW, MacKenzie EL, Mazan S, Kuratani S, Sugaharad F, Kusakabe R, Burke AC. 2013. Body wall development in lamprey and a new perspective on the origin of vertebrate paired fins. Proceedings of the National Academy of Sciences of the United States of America 110(29):11899-11904.

Turner S. 1982. A new articulated thelodont (Agnatha) from the Early Devonian of Britain. Palaeontology 25(4):879-889.

Turner S. 1991. Monophyly and interrelationships of the Thelodonti. In: Chang M-M, Liu Y-H, Zhang G-R, editors. Early Vertebrates and Related Problems of Evolutionary Biology. Beijing, China: Science Press. p 87-119.

Turner S. 1992. Thelodont lifestyles. In: Mark-Kurik E, editor. Fossil Fishes as Living Animals. Tallinn, Estonia: Academy of Science of Estonia. p 21-40.

Turner S. 2004. Early vertebrates: Analysis from microfossil evidence. In: Arratia G, Wilson MVH, Cloutier R, editors. Recent Advances in the Origin and Early Radiation of Vertebrates. München, Germany: Verlag Dr. Friedrich Pfeil. p 67-94.

Turner S, Burrow CJ, Schultze H-P, Blieck A, Reif WE, Rexroad CB, Bultynck P, Nowlan GS. 2010. False teeth: Conodont-vertebrate phylogenetic relationships revisited. Geodiversitas 32(4):545-594.

Turner S, van der Brugghen W. 1993. The Thelodonti, an important but enigmatic group of Paleozoic fishes. Modern Geology 18:125-140.

Turner S, Young GC. 1992. Thelodont scales from the Middle Late Devonian Aztec Siltstone, Southern Victoria-Land, Antarctica. Antarctic Science 4(1):89-105.

Uyeno T. 1991. Observations on locomotion and feeding of released coelacanths, *Latimeria chalumnae*. Environmental Biology of Fishes 32(1-4):267-273.

van den Boogaart JGM, Muller M, Osse JWM. 2012. Structure and function of the median finfold in larval teleosts. Journal of Experimental Biology 215(14):2359-2368.

van der Brugghen W. 1994. Over magen en staarten van thelodonten. Grondboor en Hamer(4/5):87-93.

van Eeden FJM, Granato M, Schach U, Brand M, FurutaniSeiki M, Haffter P, Hammerschmidt M, Heisenberg CP, Jiang YJ, Kane DA and others. 1996. Genetic analysis of fin formation in the zebrafish, *Danio rerio*. Development 123:255-262.

Vélez-Zuazo X, Agnarsson I. 2011. Shark tales: A molecular species-level phylogeny of sharks (Selachimorpha, Chondrichthyes). Molecular Phylogenetics and Evolution 58(2):207-217.

Vermeij GJ. 1973. Adaptation, versatility, and evolution. Systematic Zoology 22(4):466-477.

Vézina D. 1990. Les Plourdosteidae fam. nov. (Placodermi, Arthrodira) et leurs relations phylétiques au sein des Brachythoraci. Canadian Journal of Earth Sciences 27(5):677-683.

Vézina D. 1996. Placodermi (Antiarchi and Arthrodira). In: Schultze H-P, Cloutier R, editors. Devonian Fishes and Plants of Miguasha, Quebec, Canada. München, Germany: Verlag Dr. Friedrich Pfeil. p 141-148.

Vladykov VD. 1973. A female sea lamprey (*Petromyzon marinus*) with a true anal fin, and the question of the presence of an anal fin in Petromyzonidae. Canadian Journal of Zoology 51:221-224.

Vladykov VD, Kott E. 1980. Description and key to metamorphosed specimens and ammocoetes of Petromyzonidae found in the Great Lakes region. Canadian Journal of Fisheries and Aquatic Sciences 37:1616-1625.

von Dassow G, Munro E. 1999. Modularity in animal development and evolution: Elements of a conceptual framework for Evo-Devo. Journal of Experimental Zoology 285(4):307-325.

von Zittel KA, Woodward AS. 1902. Class I. Pisces. In: Eastman CR, editor. Text-Book of Palaeontology. New York, NY: McMillan and Co., Ltd. p 2-114.

Vorobyeva E, Hinchliffe R. 1996. From fins to limbs - Developmental perspectives on paleontological and morphological evidence. Evolutionary Biology 29:263-311.

Vorobyeva EI, Schultze H-P. 1991. Description and systematics of panderichthyid fishes with comments on their relationship to tetrapods. In: Schultze H-P, Trueb L, editors. Origins of the Higher Groups of Tetrapods: Controversy and Consensus Ithaca, NY: Cornell University Press. p 68-109.

Voskoboinikova OS, Kudryavtseva OY. 2014. Development of bony skeleton in the ontogeny of lumpfish *Cyclopterus lumpus* (Cyclopteridae, Scorpaeniformes). Journal of Ichthyology 54(5):301-310.

Wagner GP. 1996. Homologues, natural kinds and the evolution of modularity. American Zoologist 36(1):36-43.

Wagner GP, Altenberg L. 1996. Perspective: Complex adaptations and the evolution of evolvability. Evolution 50(3):967-976.

Wagner GP, Mezey JG. 2004. The role of genetic architecture constraints in the origin of variational modularity. In: Schlosser G, Wagner GP, editors. Modularity in

Development and Evolution. Chicago, IL: The University of Chicago Press. p 338-358.
Wagner GP, Pavlicev M, Cheverud JM. 2007. The road to modularity. Nature Reviews Genetics 8(12):921-931.
Wainwright PC, Bellwood DR, Westneat MW, Grubich JR, Hoey AS. 2004. A functional morphospace for the skull of labrid fishes: Patterns of diversity in a complex biomechanical system. Biological Journal of the Linnean Society 82(1):1-25.
Walcott CD. 1911. Cambrian geology and paleontology II - Middle Cambrian annelids. Smithsonian Miscellaneous Collections 57(5):109-144.
Walcott CD. 1931. Addenda to descriptions of Burgess Shale fossils. Smithsonian Miscellaneous Collections 85(3):1-46.
Wang BG, He LW, Ehehalt F, Geetha-Loganathan P, Nimmagadda S, Christ B, Scaal M, Huang RJ. 2005. The formation of the avian scapula blade takes place in the hypaxial domain of the somites and requires somatopleure-derived BMP signals. Developmental Biology 287(1):11-18.
Wängsjö G. 1952. The Downtonian and Devonian vertebrates of Spitsbergen. IX. Morphologic and systematic studies of the Spitsbergen cephalaspids, results of Th. Vogt's expedition 1928 and the English-Norwegian-Swedish expedition 1939. Norsk Polarinstitutt Skrifter 97:1-611.
Ward AB, Mehta RS. 2010. Axial elongation in fishes: Using morphological approaches to elucidate developmental mechanisms in studying body shape. Integrative and Comparative Biology 50(6):1106-1119.
Warren A, Currie BP, Burrow C, Turner S. 2000. A redescription and reinterpretation of *Gyracanthides murrayi* Woodward 1906 (Acanthodii, Gyracanthidae) from the Lower Carboniferous of the Mansfield Basin, Victoria, Australia. Journal of Vertebrate Paleontology 20(2):225-242.
Watson DMS. 1934. The interpretation of arthrodires. Proceedings of the Zoological Society of London 104(3):437-464.
Watson DMS. 1937. The acanthodian fishes. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 228(549):49-146.
Watson DMS. 1954. A consideration of ostracoderms. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 238(652):1-25.
Webb PW. 1975. Hydrodynamics and energetics of fish propulsion. Bulletin of the Fisheries Research Board of Canada 190:1-158.
Webb PW. 1982. Locomotor patterns in the evolution of actinopterygian fishes. American Zoologist 22(2):329-342.
Webb PW. 1984. Body form, locomotion and foraging in aquatic vertebrates. American Zoologist 24(1):107-120.
Weiss KM. 1990. Duplication with variation: Metameric logic in evolution from genes to morphology. Yearbook of Physical Anthropology 33:1-23.

Wendruff AJ, Wilson MVH. 2012. A fork-tailed coelacanth, *Rebellatrix divaricerca*, gen. et sp. nov. (Actinistia, Rebellatricidae, fam. nov.), from the Lower Triassic of Western Canada. Journal of Vertebrate Paleontology 32(3):499-511.

West-Eberhard MJ. 2003. Developmental Plasticity and Evolution. Oxford, UK: Oxford University Press.

Westoll TS. 1945a. A new cephalaspid fish from the Downtonian of Scotland, with notes on the structure and classification of ostracoderms. Transactions of the Royal Society of Edinburgh-Earth Sciences 61(2):341-357.

Westoll TS. 1945b. The paired fins of placoderms. Transactions of the Royal Society of Edinburgh 61:381-398.

Westoll TS. 1949. On the evolution of the Dipnoi. In: Jepsen GL, Mayr E, Simpson GG, editors. Genetics, Paleontology, and Evolution. Princeton, NJ: Princeton University Press. p 121-184.

Westoll TS. 1958. The lateral fin-fold theory and the pectoral fins of ostracoderms and early fishes. In: Westoll TS, editor. Studies on Fossil Vertebrates. London, UK: The Athlone Press, University of London. p 180-211.

White EI. 1935. The ostracoderm *Pteraspis* Kner and the relationships of the agnathous vertebrates. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 225:381-457.

White EI. 1946. *Jamoytius kerwoodi*, a new chordate from the Silurian of Lanarkshire, Scotland. Geological Magazine 83(2):89-97.

White EI. 1958. On *Cephalaspis lyelli* Agassiz. Palaeontology 1(2):99-105.

Whittaker J. 1990. Graphical models in applied mathematical multivariate statistics. New York, NY: John Wiley and Sons. 462 p.

Wickstead JH. 1969. Some further comments on *Jamoytius kerwoodi* White. Zoological Journal of the Linnean Society 48(3):421-422.

Wiley A. 1894. *Amphioxus* and the Ancestry of the Vertebrates. New York: MacMillan and Co.

Wiley EO, Johnson GD, Dimmick WW. 2000. The interrelationships of acanthomorph fishes: A total evidence approach using molecular and morphological data. Biochemical Systematics and Ecology 28(4):319-350.

Wilson MVH, Caldwell MW. 1993. New Silurian and Devonian fork-tailed 'thelodonts' are jawless vertebrates with stomachs and deep bodies. Nature 361(6411):442-444.

Wilson MVH, Caldwell MW. 1998. The Furcacaudiformes: A new order of jawless vertebrates with thelodont scales, based on articulated Silurian and Devonian fossils from northern Canada. Journal of Vertebrate Paleontology 18(1):10-29.

Wilson MVH, Hanke GF, Märss T. 2007. Paired fins of jawless vertebrates and their homologies across the "agnathan"-gnathostome transition. In: Anderson JS, Sues HD, editors. Major Transitions in Vertebrate Evolution. Bloomington: Indiana University Press. p 122-149.

Wilson MVH, Märss T. 2004. Toward a phylogeny of the thelodonts. In: Arratia G, Wilson MVH, Cloutier R, editors. Recent Advances in the Origin and Early

Radiation of Vertebrates. München, Germany: Verlag Dr. Friedrich Pfeil. p 95-108.
Wilson MVH, Märss T. 2009. Theolodont phylogeny revisited, with inclusion of key scale-based taxa. Estonian Journal of Earth Sciences 58(4):297-310.
Wilson MVH, Märss T. 2012. Anatomy of the Silurian thelodont *Phlebolepis elegans* Pander. Estonian Journal of Earth Sciences 61(4):261-276.
Winchell CJ, Martin AP, Mallatt J. 2004. Phylogeny of elasmobranchs based on LSU and SSU ribosomal RNA genes. Molecular Phylogenetics and Evolution 31(1):214-224.
Winther RG. 2001. Varieties of modules: Kinds, levels, origins, and behaviors. Journal of Experimental Zoology 291(2):116-129.
Wisner RL, McMillan CB. 1988. A new species of hagfish, genus *Eptatretus* (Cyclostomata, Myxinidae), from the Pacific Ocean near Valparaiso, Chile, with new data on *E. bischoffi* and *E. polytrema*. Transactions of the San Diego Society of Natural History 21(14):227-244.
Wisner RL, McMillan CB. 1990. Three new species of hagfishes, genus *Eptatretus* (Ciclostomata, Myxinidae), from the Pacific coast of North America, with new data on *E. deani* and *E. stoutii*. Fishery Bulletin 88(4):787-804.
Wisner RL, McMillan CB. 1995. Review of new-world hagfishes of the genus *Myxine* (Agnatha, Myxinidae) with descriptions of 9 new species. Fishery Bulletin 93(3):530-550.
Withers PC. 1981. Physiological correlates of limblessness and fossoriality in scincid lizards. Copeia 1981(1):197-204.
Woodward AS. 1900a. On a new ostracoderm (*Euphanerops longaevus*) from the Upper Devonian of Scaumenac Bay, Province of Quebec, Canada. The Annals and Magazine of Natural History, Seventh Series 5(29):416-419.
Woodward AS. 1900b. Reviews - Dr. Traquair on Silurian fishes. Report on fossil fishes collected by the geological survey of Scotland in the Silurian rocks of the south of Scotland. By Ramsay H. Traquair, M.D., LL.D., F.R.S. Trans. Roy. Soc. Edinb., vol. xxxix, pp. 827-864, pls. i-v (December, 1899). Geological Magazine 7(2):66-72.
Wright GM, Keeley FW, DeMont MW. 1998. Hagfish cartilage. In: Jørgensen JM, Lomholt JP, Weber RE, Malte H, editors. The Biology of Hagfishes. London, UK: Chapman & Hall. p 160-170.
Xu GH, Zhao LJ, Shen CC. 2015. A Middle Triassic thoracopterid from China highlights the evolutionary origin of overwater gliding in early ray-finned fishes. Biology Letters 11(1):5.
Xu QS, Ma F, Wang YQ. 2005. Morphological and 12S rRNA gene comparison of two *Branchiostoma* species in Xiamen waters. Journal of Experimental Zoology Part B-Molecular and Developmental Evolution 304B(3):259-267.
Yalden DW. 1985. Feeding mechanisms as evidence for cyclostome monophyly. Zoological Journal of the Linnean Society 84:291-300.

Yamanoue Y, Setiamarga DHE, Matsuura K. 2010. Pelvic fins in teleosts: Structure, function and evolution. Journal of Fish Biology 77(6):1173-1208.

Yano T, Tamura K. 2013. The making of differences between fins and limbs. Journal of Anatomy 222(1):100-113.

Yarrell W. 1836. A History of British Fishes. Vol. II. London: J.V. Voorst. 472 p.

Yonei-Tamura S, Abe G, Tanaka Y, Anno H, Noro M, Ide H, Aono H, Kuraishi R, Osumi N, Kuratani S and others. 2008. Competent stripes for diverse positions of limbs/fins in gnathostome embryos. Evolution & Development 10(6):737-745.

Young GC. 1982. Devonian sharks from south-eastern Australia and Antarctica. Palaeontology 25(4):817-843.

Young GC. 1991. The first armoured agnathan vertebrates from the Devonian of Australia. In: Chang M-M, Liu Y-H, Zhang G-R, editors. Early Vertebrates and Related Problems of Evolutionary Biology. Beijing, China: Science Press. p 67-85.

Young GC. 1997. Ordovician microvertebrate remains from the Amadeus Basin, central Australia. Journal of Vertebrate Paleontology 17(1):1-25.

Young GC. 2008. The relationships of antiarchs (Devonian placoderm fishes) - Evidence supporting placoderm monophyly. Journal of Vertebrate Paleontology 28(3):626-636.

Young GC. 2010. Placoderms (armored fish): Dominant vertebrates of the Devonian period. Annual Review of Earth and Planetary Sciences 38:523-550.

Young GC, Long JA, Ritchie A. 1992. Crossopterygian fishes from the Devonian of Antarctica: Systematics, relationships and biogeographic significance. Records of the Australian Museum Supplement 14:1-77.

Young NM, Hallgrímsson B. 2005. Serial homology and the evolution of mammalian limb covariation structure. Evolution 59(12):2691-2704.

Young NM, Wagner GP, Hallgrímsson B. 2010. Development and the evolvability of human limbs. Proceedings of the National Academy of Sciences of the United States of America 107(8):3400-3405.

Yu XB. 1998. A new porolepiform-like fish, *Psarolepis romeri*, gen. et sp. nov. (Sarcopterygii, Osteichthyes) from the lower Devonian of Yunnan, China. Journal of Vertebrate Paleontology 18(2):261-274.

Zajíc J. 1995. Some consequences of recent investigations on the family Acanthodidae Huxley, 1861. Geobios 28(Suppl. 2):167-169.

Zajíc J. 1998. Acanthodians of the Bohemian limnic Stephanian. Czech Geological Survey Special Papers(10):1-45.

Zangerl R. 1981. Volume 3A - Chondrichthyes I - Paleozoic Elasmobranchii. Schultze H-P, editor. Stuttgart, New York: Gustav Fischer Verlag. 115 p.

Zangerl R. 1997. *Cervifurca nasuta* n. gen. et sp., an interesting member of the Iniopterygidae (Subterbranchialia, Chondrichthyes) from the Pennsylvanian of Indiana, U.S.A. Fieldiana, Geology N.S.(35):1-24.

Zangerl R, Case GR. 1973. Iniopterygia, a new order of chondrichthyan fishes from the Pennsylvanian of North America. Fieldiana Geology Memoirs 6:1-67.

Zelditch ML. 1987. Evaluating models of developmental integration in the laboratory rat using confirmatory factor analysis. Systematic Zoology 36(4):368-380.

Zelditch ML, Swiderski DL, Sheets HD. 2012. Geometric Morphometrics for Biologists: A Primer. Second edition. London, UK: Elsevier Academic Press. 478 p.

Zelditch ML, Wood AR, Bonett RM, Swiderski DL. 2008. Modularity of the rodent mandible: Integrating bones, muscles, and teeth. Evolution & Development 10(6):756-768.

Zelditch ML, Wood AR, Swiderski DL. 2009. Building developmental integration into functional systems: Function-induced integration of mandibular shape. Evolutionary Biology 36(1):71-87.

Zhang XG, Hou XG. 2004. Evidence for a single median fin-fold and tail in the Lower Cambrian vertebrate, *Haikouichthys ercaicunensis*. Journal of Evolutionary Biology 17(5):1162-1166.

Zhu M, Ahlberg PE. 2004. The origin of the internal nostril of tetrapods. Nature 432(7013):94-97.

Zhu M, Gai Z. 2007. Phylogenetic relationships of galeaspids (Agnatha). Frontiers of Biology in China 2(2):151-169.

Zhu M, Schultze H-P. 1997. The oldest sarcopterygian fish. Lethaia 30(4):293-304.

Zhu M, Schultze H-P. 2001. Interrelationships of basal osteichthyans. In: Ahlberg PE, editor. Major Events in Early Vertebrate Evolution: Palaeontology, Phylogeny, Genetics and Development. London: Taylor & Francis. p 289-314.

Zhu M, Yu XB. 2002. A primitive fish close to the common ancestor of tetrapods and lungfish. Nature 418(6899):767-770.

Zhu M, Yu XB, Ahlberg PE. 2001. A primitive sarcopterygian fish with an eyestalk. Nature 410(6824):81-84.

Zhu M, Yu XB, Ahlberg PE, Choo B, Lu J, Qiao T, Qu QM, Zhao WJ, Jia LT, Blom H and others. 2013. A Silurian placoderm with osteichthyan-like marginal jaw bones. Nature 502(7470):188-193.

Zhu M, Yu XB, Choo B, Qu QM, Jia LT, Zhao WJ, Qiao T, Lu J. 2012a. Fossil fishes from China provide first evidence of dermal pelvic girdles in osteichthyans. PLoS One 7(4):9.

Zhu M, Yu XB, Choo B, Wang JQ, Jia LT. 2012b. An antiarch placoderm shows that pelvic girdles arose at the root of jawed vertebrates. Biology Letters 8(3):453-456.

Zhu M, Yu XB, Janvier P. 1999. A primitive fossil fish sheds light on the origin of bony fishes. Nature 397(6720):607-610.

Zhu M, Yu XB, Wang W, Zhao WJ, Jia LT. 2006. A primitive fish provides key characters bearing on deep osteichthyan phylogeny. Nature 441(7089):77-80.

Zhu M, Zhao WJ, Jia LT, Lu J, Qiao T, Qu QM. 2009. The oldest articulated osteichthyan reveals mosaic gnathostome characters. Nature 458(7237):469-474.

Zidek J. 1993. Acanthodii. In: Benton MJ, editor. The Fossil Record 2. London, UK: Chapman & Hall. p 589-592.

Žigaitė Ž, Blieck A. 2013. Palaeobiogeography of Early Palaeozoic vertebrates. In: Harper DAT, Servais T, editors. Early Palaeozoic Biogeography and Palaeogeography. Bath: Geological Society Publishing House. p 449-460.

Zintzen V, Roberts CD, Shepherd L, Stewart AL, Struthers CD, Anderson MJ, McVeagh M, Noren M, Fernholm B. 2015. Review and phylogeny of the New Zealand hagfishes (Myxiniformes: Myxinidae), with a description of three new species. Zoological Journal of the Linnean Society 174(2):363-393.

Zug G. 1979. The endoskeleton: The comparative anatomy of the girdles, the sternum, and the paired appendages. In: Wake MH, editor. Hyman's Comparative Vertebrate Anatomy, Third edition. Chicago, IL: The University of Chicago Press. p 238-264.

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